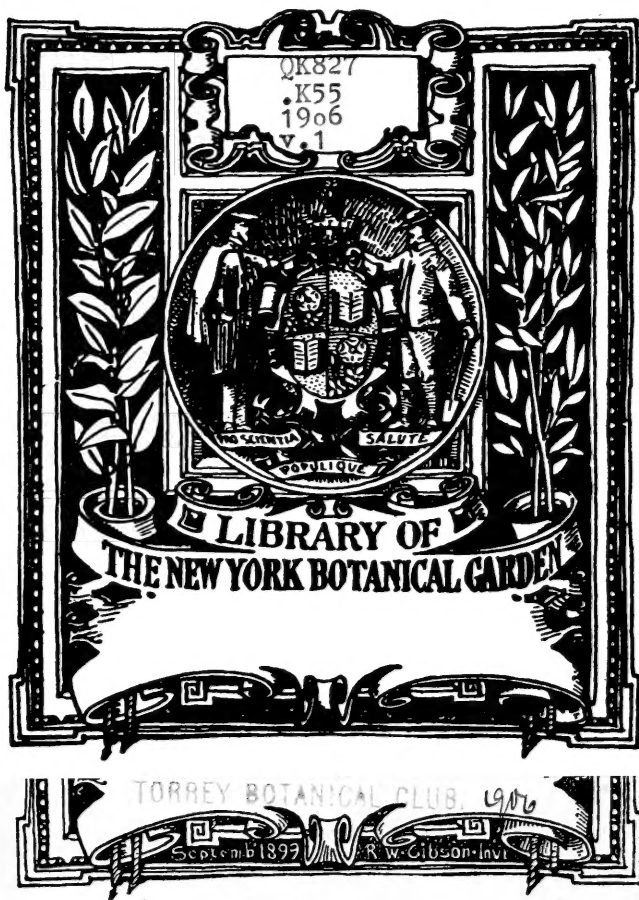


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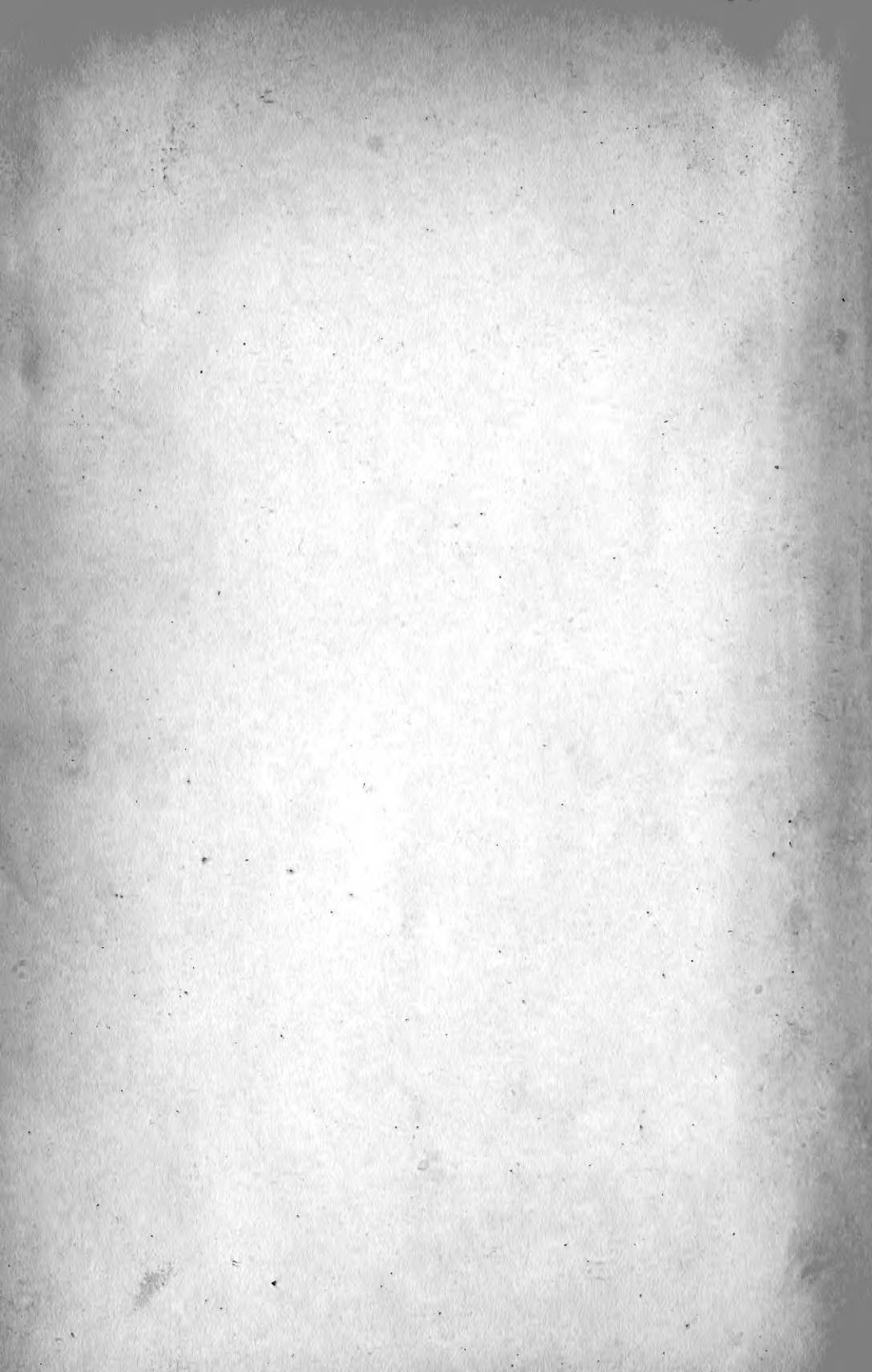
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Dr. Kölmacher.

HANDBOOK OF FLOWER POLLINATION

BASED UPON

HERMANN MÜLLER'S WORK
'THE FERTILISATION OF
FLOWERS BY INSECTS'

BY

DR. PAUL KNUTH

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MEMBER OF THE BOTANICAL SOCIETY DODONAEA IN GHENT

TRANSLATED BY

J. R. AINSWORTH DAVIS, M.A.

TRINITY COLLEGE, CAMBRIDGE

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VOLUME I

INTRODUCTION AND LITERATURE

WITH 81 FIGURES IN THE TEXT

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TO THE MEMORY OF
CHRISTIAN KONRAD SPRENGEL

FORMERLY RECTOR OF THE GREAT LUTHERAN TOWN-SCHOOL IN SPANDAU

BORN AT BRANDENBURG ON THE HAVEL IN 1750

DIED AT BERLIN ON APRIL 7TH, 1816

AND

DR. HERMANN MÜLLER

FORMERLY PROFESSOR IN THE REALSCHULE AT LIPPSTADT IN WESTPHALIA

BORN AT MÜHLBERG IN THURINGIA ON SEPTEMBER 23RD, 1829

DIED AT PRAD IN THE TYROL ON AUGUST 25TH, 1883

CHRISTIAN KONRAD SPRENGEL and HERMANN MÜLLER were characterized by untiring diligence and ardour for research, incomparable powers of observation, and extraordinary acuteness in the interpretation of the phenomena of Flower Pollination. With this was united in a conspicuous degree the ability to describe their discoveries in a most admirable manner. Their fundamentally important works on Flower Pollination are now, therefore, an inexhaustible source of instruction and enjoyment, as they must always be. This book, which shows the present position of the Science of Flower Pollination, is dedicated to the memory of these two great investigators.

[illegible]

1940-1941

AUTHOR'S PREFACE

TWENTY-FIVE years have passed since the appearance of Hermann Müller's admirable book on 'The Fertilisation of Flowers by Insects and their Reciprocal Adaptations'¹. It has long been out of print, and it seemed to me to be worthy of republication with notes, like the fundamental work of Christian Konrad Sprengel: *Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen* (Berlin, 1793), which I brought out some years ago in Ostwald's *Klassiker der exakten Naturwissenschaften* (vols. xlviii-li)². The further, however, I entered into the subject, the more I became convinced that the observations of later investigators, following in the steps of Müller during the last two decades, and developing this branch of botany in a remarkable manner, have given us such abundance of new material that the necessary notes and additions would considerably exceed the original contents of Müller's book. I accordingly resolved to write an entirely new work, founded upon Hermann Müller's 'Fertilisation of Flowers by Insects,' after satisfactory arrangements had been made with his representatives.

The fruitfulness of the investigations made during the last two decades on the relations between the structure and environment of flowers, and the widening of the circle of those who take an active part in these investigations, have added to the difficulty of the task of collating the enormous quantity of available material. To accomplish this it was necessary to devote three years of uninterrupted labour, during which there appeared numerous, and in part extremely important, new publications on Flower Pollination, which had to be taken into consideration. Literary activity, however, quite unlike scientific investigation, demands a conclusion, and therefore it seemed to me inexpedient to delay any longer the publication of the work. The memoirs that appeared on the subject during the printing of my work were considered as far as possible, especially when they afforded a solution of contradictions occurring in the statements of different observers in regard to the same flower. During the whole time spent in writing this work, I have been constantly engaged

¹ 'Die Befruchtung der Blumen durch Insekten und die gegenseitigen Anpassungen beider, Leipzig, 1873, Wilhelm Engelmann. English Translation by D'Arcy W. Thompson, 1883.

² Leipzig, 1894, Wilhelm Engelmann.

in trying to clear up such contradictions by my own investigations, and in endeavouring by my own research to increase our knowledge of floral adaptations, and of the visitors to our flowers, so that this book will seldom be consulted in vain by any one who desires information of this sort with regard to our indigenous or cultivated plants.

It would, however, have been impossible for me to bring the work to a conclusion in the comparatively short space of three years, if I had not been able to make use of several excellent recent works on Flower Pollination, especially those of Kerner, Loew, and Ludwig, and unless I had been given most friendly assistance by numerous flower specialists, and by my other botanical and entomological friends, who were always ready to help me in every possible way. I therefore take this opportunity of renewing my thanks to all these, especially to the following gentlemen:— D. ALFKEN in Bremen, O. APPEL in Würzburg, J. BEHRENS in Karlsruhe, F. BUCHENAU in Bremen, J. HENRY BURKILL in Kew, C. CORRENS in Tübingen, F. DAHL in Berlin, K. v. DALLA TORRE in Innsbruck, F. DELPINO in Naples, O. EKSTAM in Tromsö, TH. FRIES in Upsala, A. GLOY in Kiel, A. HANSRIG in Prague, J. H. HART in Port of Spain (Trinidad), F. HILDEBRAND in Freiburg i. B., A. KERNER VON MARILAUN in Vienna, O. KIRCHNER in Hohenheim, A. KNEUCKER in Karlsruhe, E. LOEW in Berlin, F. LUDWIG in Greiz, J. MACLEOD in Ghent, P. MAGNUS in Berlin, TH. MEEHAN in Germantown, Philad. (U.S.A.), F. MÜLLER (†) in Blumenau (Brazil), G. NATHORST in Stockholm, F. PLATEAU in Ghent, K. RECHINGER in Vienna, CH. ROBERTSON in Carlinville, Ill. (U. S. A.), CHR. SCHRÖDER in Itzehoe, A. SCHULZ in Halle, G. F. SCOTT-ELLIOT in Glasgow, P. STOLZENBURG in Kiel, J. URBAN in Berlin, C. VERHOEFF in Bonn, E. WARMING in Copenhagen, and C. WARNSTORF in Neu-Ruppin. I also carried on at times a very extensive correspondence on the subject of this book, especially with Herren ALFKEN, APPEL, KIRCHNER, LOEW, and LUDWIG.

It was my intention to embellish this work with portraits and autographs of all the most distinguished specialists in flower pollination, but it was impossible to obtain photographs of all. I have, therefore, confined myself to giving portraits of those to whom we are indebted in the highest degree for the advancement of the subject: i.e. J. G. Kölreuter, Charles Darwin, H. and F. Müller, F. Delpino, F. Hildebrand, and S. Axell. Unfortunately no portrait of the grand master of our science, Christian K. Sprengel, was to be had. There is given, therefore, in the absence of this, a reduced facsimile of the characteristic title-page of his book 'Das entdeckte Geheimnis.'

I have endeavoured, so far as possible, to make use of the original memoirs of authors in recounting their observations, and have also, when practicable, adhered to the terms used by them, but I was not able to see all the original works on Flower Pollination, in particular the more recent

works in Italian and French. I have, therefore, frequently been obliged to content myself with information derived from references in the 'Botanischer Jahresbericht' (1883 to 1895), and the 'Botanisches Centralblatt.' Some works had to be left altogether unnoticed, as I was not able to get any information as to their contents. A few have no doubt escaped me altogether, but I hope to have attained at least relative completeness.

In course of the preparation of the material, it appeared that the work would be too comprehensive for a single volume. I determined, therefore, to publish in the following divisions.—

1. Introduction and Literature.
2. The Observations in Flower Pollination hitherto made in Europe and in the Arctic regions.
 - (a) Ranunculaceae to Compositae.
 - (b) Lobeliaceae to Coniferae.
3. Observations in Flower Pollination made outside Europe.

In the introduction, I have given, in the first place, a short survey of the historical development of flower pollination. In doing this I was chiefly concerned with introducing the most prominent facts in this sphere of research, especially the labours of Kölreuter and Sprengel, and the development of the floral theory which is associated with the names of Sprengel, Knight, Darwin, Hildebrand, Axell, Delpino, and Hermann Müller. This short survey will sufficiently elucidate the present standpoint of flower pollination. I was freed from the necessity of exhaustively considering the historical development of this science by the excellent work of E. Loew, 'Einführung in die Blütenbiologie auf historischer Grundlage' (Berlin, 1895). In this work the subject is treated at great length, and accordingly Loew's 'Introduction' forms a necessary supplement to my handbook.

In the second division of the introduction, besides my own writings and those of Hermann Müller, I have made most use of the works of Charles Darwin, F. Delpino, W. O. Focke, F. Hildebrand, A. Kerner, O. Kirchner, E. Loew, F. Ludwig, H. von Mohl, Fritz Müller, Christian K. Sprengel, Aug. Schulz, and E. Warming; and from these an idea of the present position of flower pollination is obtained. The lists of self-sterile, self-fertile, and cleistogamous flowers may not, however, be quite complete.

The compilation of the literature of flower pollination was made much easier by the following: 'Bibliography' in D'Arcy W. Thompson's translation of Hermann Müller's 'Befruchtung der Blumen durch Insekten' ('The Fertilisation of Flowers,' London, 1883, pp. 599-630), which contains most references to literature up to the year 1882; MacLeod's 'Lijst van

Boeken, Verhandlingen, enz. omtrent de bevruchting der Bloemen, van 1883 tot 1889 verschenen' (Bot. Jaarb. Dodonaea, Ghent, ii, 1890, pp. 195-254); and lastly, the 'Litteraturverzeichniss (1883-93)' in Loew's 'Blütenbiologische Floristik' (Stuttgart, 1894, pp. 4-18). I have supplemented these notices of the literature especially by working through the references published by v. Dalla Torre in Just's 'Botanischer Jahresbericht' from 1883 to 1895, and placed at my disposal by the author, and also the 'Neue Litteratur' in the 'Botanisches Centralblatt' from 1880 till October 1, 1897. An appendix gives the works on flower pollination that have appeared during the printing of the first volume, up to April, 1898. Here also are named a few of the oldest works on the sexuality and the fertilization of flowers, which I had at first overlooked, as well as the literature on perception of form and colour, and on the olfactory and visual powers of insects, mostly from H. J. Kolbe's 'Einführung in die Kenntnis der Insekten' (Berlin, 1893). The bibliography as here presented should be moderately complete, but I cannot in every case vouch that the titles are absolutely correct, as the original works were not always available, and some of the sources on which I had to depend contain numerous printers' errors.

The works that appeared during the preparation and the printing of this handbook have been, as I have already said, taken into consideration as far as possible. The notices which J. Behrens has published on Kölreuter (Verh. Natw. Ver., Karlsruhe, 1894), and the important investigations of F. Plateau which have been published under the title 'Comment les fleurs attirent les insectes' (Bul. Acad. roy., Bruxelles, 1895-7), are discussed in an appendix to the introduction.

The second volume contains descriptions of the structure of flowers, and notices of the flower visitors hitherto observed in Europe and in the Arctic regions, and of their relations with the flowers they visit, following closely the accounts of the observers who first described the facts. I have, in particular, left unaltered, so far as possible, Hermann Müller's descriptions of flowers, as an account by this investigator cannot be safely modified: I have, however, usually made slight abbreviations. While descriptions of the structure of flowers belonging to indigenous European species have generally been retained intact, and their visitors given as fully as possible, I have only briefly indicated observations made in Europe on cultivated but non-indigenous plants. A fuller description will be given of these in the third volume of this work, but they could not be altogether omitted in the second, as it was impossible to distinguish sharply between indigenous, acclimatized, and cultivated species. I have, therefore, given short accounts of all observations made in Europe on plants that are not indigenous. On the other hand, I have left unnoticed all investigations which, though described in European periodicals, refer to extra-European regions. It is obvious that in dealing with such an

immense amount of material, I must now and then have overlooked observations on the flower pollination of foreign species. But in such cases these will be found in the third volume. On the other hand, a comparative review has been given in the second volume of Ekstam's accounts of flowers and their guests in Nova Zemlia, the observations of Lindman on floral structure and pollinating agents made in the Dovrefjeld region of the Scandinavian Highlands, the similar researches of Warming with regard both to this region and Greenland, and the works of Aurivillius on insect life in the high North.

Only the most important of the very numerous descriptions given in Kerner's 'Natural History of Plants' have been referred to in the second volume of this handbook, as most of them are briefly mentioned in Volume I. A complete purview of the very extensive material gathered together in the 'Natural History of Plants' has not been attempted, as Kerner's work is very widely known.

In describing the natural orders of plants from the point of view of flower pollination, the indigenous European forms are dealt with at greatest length; extra-European species are referred to only occasionally, as they are reserved for treatment in the following volume.

I have endeavoured in this handbook to establish generic characters in flower pollination, as I previously did in my work 'Blumen und Insekten auf den nordfriesischen Inseln'; yet this has not been practicable in all cases, for the observations on some species were too imperfect.

It was not always possible with the resources at my disposal to determine the authors of names of species; and as reference to the biologist in whose work I found a name did not always furnish the desired information, a few species of plants have had to remain without an author's name.

Besides observations on insect-visits recorded in works specially devoted to flower pollination, there are also included records from numerous purely entomological works and treatises, so far as these leave no doubt as to the species of plant concerned¹. Among these works are those mentioned in the bibliography (vol. i, p. 212) under the names of the following authors:— Alfken, André, Aurivillius, Bonnier, Cobelli, v. Dalla Torre, Dours, Ducke, Entleutner, Frey, Frey-Gessner, v. Fricken, Friese, Gerstaecker, Handlirsch, Hoffer, Holmgren, Koch, Kohl, Krieger, Leege, Marquard, Morawitz, Nylander, Pérez, Redtenbacher, Rössler, Saunders, Schenck, Schletterer, Schiner, Schmiedeknecht, Schultess-Rechberg, Sickmann, Smith, Thomson, and Wüstnei.

¹ Ambiguous references are neglected,—such as: 'Especially in some species of *Centaurea* and *Sedum*.' An exception is made, however, in the case of *Salix*, as experience shows that insects visit the various species indiscriminately.

Some of these works, for instance those of Alfken, Dalla Torre, Frey, Friese, Hoffer, Krieger, Morawitz, Schletterer, and Sickmann, contain in places an amazing amount of material for use by the flower specialist, and frequently afford the only available information as to visitors to flowers. Others, on the contrary, as, for instance, André's work, which is in many volumes, contain only a few useful notices. There are numerous other entomological works, especially in French and Italian, which might have been referred to, but to have done so would have greatly increased the toil of compilation; and it is questionable if the result would have repaid the labour. Some, indeed, of the works that were looked into contained no useful information at all, as, for instance, Aurivillius (*Grönlands insektfauna*; Vet.-Ak. Bih., Stockholm, Vol. xv, Ser. 4, Nr. 1, pp. 1-33) and F. Chevrier (*Description des Chrysides du Bassin du Léman*, Geneva, 1862)¹.

Herr D. Alfken has placed at my disposal his valuable observations on the visits of insects to flowers in the neighbourhood of Bremen. Some observations of Hans Hoppner, that also refer to the neighbourhood of Bremen, are added. Further, Herr Alfken has communicated to me, in addition to his previously published observations on the Island of Juist, a number of new ones.

Besides my own observations on the visits of insects to flowers, and in addition to those of Borgstette, Buddeberg, Burkill, Cobelli, Darwin, Delpino, Ekstam, Heinsius, Lindman, Loew, MacLeod, Hermann Müller, Plateau, Rathay, Ricca, Schneider, A. Schulz, Scott-Elliot, Sprengel, Verhoeff, de Vries, Willis, and Wittrock, there is a very considerable mass of work containing material useful in studying flower pollination; so that here again only a relative independence can be claimed. The 'tedious' lists of visitors, in which thousands of individual observations are set down, form the indispensably necessary statistical material upon which to base our knowledge of the relations subsisting between groups of flowers and insects. They afford an insight into the connection between the structure of flowers and the anatomical characters of insects; they tell us that everywhere flowers are sought out in preponderating majority by such insects as are modified in adaptation to them. I reserve this statistical material for working up afresh.

It must be admitted that in the enumeration of visitors, the record

¹ There were also no observations on flower pollination in works that I looked through by M. J. Pérez (*Contributions à la faune des Apiaries de France*, II^e partie, Parasites.—Actes soc. linn. Bordeaux, 1883) and by Ruggero Cobelli (*Gli imenotteri di Trentino*, Fasc. I: Formicidae, Rovereto, 1887; Fasc. II: Tenthredinidae, Apidae, Chrysidae, Pompilidae, Scoliidae, Mutillidae, Sapygidae, 1891; Fasc. III: Vespidae.—Sphegidae, 1893; Fasc. IV: Evanidae, Cynipidae, Chalcididae, Proctotrupidae, Ichneumonidae, Braconidae, 1897).

of the way in which the visit is effected is frequently not sufficiently detailed. There is often a similar lack of detail with regard to the numbers of visitors to a species and the constancy of their visits. This, however, is due to the fact that the authors whose observations are embodied have not given particulars. In this handbook an attempt is made to give a relatively complete account of visitors to the various species of plants, so as to determine their circle of guests, and therefore all records, however imperfect, are cited. For the most part, however, the kind of activity, and the numbers and constancy of the insect visitors, are indicated by the following contractions:—‘skg.’ (sucking), ‘nect-lkg.’ (nectar-licking), ‘po-cltg.’ (pollen-collecting), ‘po-dvg.’ (pollen-devouring), and ‘freq.’ (frequent). From these symbols one may almost always recognize distinctly whether the visitors were acting as pollinators or not, and a more exhaustive account of the behaviour of the insects during their visits to flowers of simple structure is therefore, in most cases, quite unnecessary. Moreover, it would greatly add to the size of this already voluminous work. Such details have only been given in the case of flowers with distinctly complicated adaptations of the floral leaves, where a more exhaustive description of the relations seemed necessary. An effort has been made to arrange the observations according to the geographical position of the districts in which they were made, though this could not always be carried out consistently.

In naming and arranging the insects I have made use of the following works.—

- C. G. DE DALLA TORRE. *Catalogus Hymenopterorum hucusque descr. syst. et syn.* Leipzig, 1892 on. (So far as published.)
- J. R. SCHINER. *Fauna Austriaca. Die Fliegen (Diptera).* 2 Bde. Wien, 1862 and 1864. JOS. MIK, *Verzeichnis der Arten-Namen, welche in SCHINER'S Fauna Austriaca enthalten sind.* Wien, 1887.
- A. PUTON. *Catalogue d'Hémiptères de la Faune paléarctique.* 3^e éd. Caen, 1886.
- C. BRUNNER V. WATTENWYL. *Prodromus der europäischen Orthopteren.* Leipzig, 1882.
- G. SEIDLITZ. *Fauna baltica. Die Käfer der deutschen Ostseeprovinzen Russlands.* 2. Aufl. Königsberg, 1891. (Where this work did not suffice the two following were used.)
- G. SEIDLITZ. *Fauna transsilvanica. Die Käfer Siebenbürgens.* Königsberg, 1887.
- M. GEMMINGER et B. DE HAROLD. *Catalogus Coleopterorum hucusque descriptorum synonymicus et systematus.* München, 1868-76.
- O. STAUDINGER und M. WOCKE. *Katalog der Lepidopteren des europäischen Faunengebietes.* Dresden, 1871.
- M. ROSTOCK. *Neuroptera germanica.* Zwickau, 1888.

The visitors of flowers are arranged alphabetically in orders, families, genera, and species. A revision of the insects observed by me visiting flowers, as detailed in earlier writings, has been undertaken by the following:—D. Alfken, Bremen; A. Costa, Naples; F. Dahl, Kiel; V. von

Röder, Hoym (Anhalt); C. Verhoeff, Bonn; W. Wüstnei, Sonderburg (Alsen). To these gentlemen I here offer my renewed thanks.

On the other hand, the records of flower visitors are not taken from works which deal with the flower pollination of a definite, circumscribed region. The following are among these.—

HERMANN MÜLLER, *Alpenblumen* (Leipzig, 1881),

P. KNUTH, *Blumen und Insekten auf den nordfriesischen Inseln* (Kiel and Leipzig, 1894),

J. MACLEOD, *De Pyreneeënbloemen en hare bevruchting door insecten* (Ghent, 1891), and

J. MACLEOD, *De bevruchting der bloemen in het Kempisch gedeelte van Vlaanderen* (Ghent, 1893 and 1894)¹.

The observations set forth in these writings are, for the most part, only referred to in this handbook, and the flower visitors that are recorded are only indicated by reference to the chief groups to which they belong. These books are necessary for every student of flower pollination, to supplement the facts narrated in this handbook.

The extraordinarily heavy and lengthy task of editing the lists of visitors was undertaken by D. Alfken of Bremen, with praiseworthy readiness. He has had the pleasure of receiving help in this work from the following gentlemen.—

H. FRIESE in Innsbruck (Bees),

F. KONOW in Teschendorf (Saw-flies),

R. KRIEGER in Leipzig (Ichneumons),

G. KÜNNEMANN in Oldenburg (Beetles),

V. VON RÖDER in Hoym (Flies),

A. SCHLETTERER in Innsbruck (Digging-wasps), and

O. STAUDINGER in Dresden-Blasewitz (Lepidoptera).

In writing the names of insects, Alfken has adhered to the rules that were laid down in the proceedings of the German Zoological Society in 1894 (p. 94), in which it is said (Par. 13 d): 'It is desirable always to write specific names with a small initial letter, following the example of English and American zoologists.'

In recent years much attention has been paid to the subject of synonymy in the names of insects. It has, however, not been possible for me always to accept the newer names, which are justified by the researches of recent years, and therefore are now the commonly used terms in entomological works, in place of the older ones employed by Hermann Müller, Loew, myself, &c. When the second volume of this work, which preceded the first volume, was in course of preparation, the naming of insects was not conducted in conformity with a definite plan, and the matter was still under discussion.

¹ 'The Flora of Dumfriesshire,' by Scott-Elliot (Dumfries, 1896), also deals with flower visitors, and these, again, will only be indicated in the present work.

On account of the simultaneous use of older and newer names, there is the awkwardness that one and the same insect appears in the lists of visitors under different names; e.g., *Anthophora pilipes* *F.* and *Podalirius acervorum* *L.* Yet this inconvenience is minimized inasmuch as at the end of the second volume there is given a systematic and alphabetical list of the insects mentioned as visitors of flowers and the flowers visited by them, with reference to the synonyms. The flower visitors are mentioned in the alphabetical sequence of the orders, families, genera, and species of insects, and at the same time both the older and newer specific terms are given.

In doubtful cases, where the correct name could not be determined, the old name has been left; thus, for instance, *Limonius cylindricus* *Payk.* is mentioned by Hermann Müller as a visitor of *Batrachium aquaticum*. This beetle may be *L. nigripes* *F.* or *L. cylindricus* *L.*, but *L. cylindricus* *Payk.* has been left. Similarly, *Halictus albipes* *F.* and *H. longulus* *Sm.* are mentioned in the lists: both are certainly identical with *H. calceatus* *Scop.*, but are still considered as distinct by some investigators. Here again, therefore, the old names have been left, the genus *Halictus* being still in need of revision.

In other cases, the names of visitors mentioned by a particular observer are synonymous. For instance, *Osmia aenea* *L.* and *O. caerulea* *L.* are mentioned by the same writer as visitors of *Lamium album*. In such a case the name (usually the older one) is chosen which is made use of in the works on which modern nomenclature is founded. Names of insects that are quite doubtful are omitted.

Most of the illustrations are taken from the works of Hermann Müller; others are from the works of Darwin, Engler and Prantl, Hildebrand, Kerner, Loew, MacLeod, Warming, and from my own earlier publications. A considerable number have been made from nature for the handbook, or have been drawn under my direction.

The references to literature on the various groups and species of plants are confined to the chief writings dealing with the plants in question. A complete enumeration of all the works which refer to every species of plant would have taken far too much space. Notices that are not referred to in the text may in most cases be found by the use of the index to the list of literature, which Dr. Appel¹ has drawn up in a most careful manner.

The abbreviations of references to literature used in the text are usually self-explanatory; in doubtful cases, the literature on flower pollination at the end of the first volume will give particulars. The following

¹ Dr. Appel also helped me in reading the proofs, and prepared the greater part of the index to the Introduction: for which favours I would here repeat my hearty thanks.

abbreviations are employed with reference to works or magazines that are frequently cited, in cases where fuller references are not given.—

1. PERIODICALS (chiefly referred to in the list of literature) ¹.

- Abh. natw. Ver., Bremen*: Abhandlungen, herausgegeben vom naturwissenschaftlichen Verein zu Bremen.
- Acad. Nat. Sci., Philadelphia*: Proceedings of the Academy of Natural Sciences of Philadelphia.
- Atti Soc. ital. sc. nat., Milano*: Atti della Società italiana di scienze naturali. Milano.
- Ber. D. bot. Ges., Berlin*: Berichte der Deutschen botanischen Gesellschaft. Berlin.
- Bot. Centralbl., Cassel*: Botanisches Centralblatt. Cassel. *Beiheft.* refers to the Beihefte, which (as a distinct publication) commenced in 1891.
- Bot. Gaz., Chicago*: J. M. COULTER'S Botanical Gazette. Chicago.
- Bot. Jaarb. Dodonaea, Ghent*: Botanisch Jaarboek uitgegeven door het Kruidkundig Genootschap 'Dodonaea' te Ghent.
- Bot. Jahrb., Leipzig*: Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie, herausgegeben von A. ENGLER. Leipzig.
- Bot. Ztg., Leipzig*: Botanische Zeitung. Leipzig.
- Bull. Torrey Bot. Cl., New York*: Bulletin of the Torrey Botanical Club. New York.
- Bul. soc. bot., Paris*: Bulletin de la société botanique (de France, de Genève, de Lyon).
- Bul. soc. linn., Paris*: Bulletin mensuel de la société linnéenne de Paris.
- C.-R. Acad. sci., Paris*: Comptes-rendus hebdomadaires des séances de l'Académie des sciences. Paris.
- D. bot. Monatschr., Arnstadt*: Deutsche botanische Monatschrift. Arnstadt.
- Gard. Chron., London*: Gardeners' Chronicle. London.
- Gartenflora, Berlin*: Gartenflora. Berlin.
- Jahrb. wiss. Bot., Leipzig*: Jahrbücher für wissenschaftliche Botanik, herausgegeben von PFEFFER u. STRASBURGER. Leipzig.
- J. Linn. Soc. Bot., London*: Journal of the Linnean Society of London, Botany.
- Justs bot. Jahresber., Leipzig*: Justs botanischer Jahresbericht. Leipzig.
- Malpighia, Genova*: Malpighia, Genova.
- Nuovo Giorn. bot. ital., Firenze*: Nuovo Giornale botanico italiano, nuova serie. Memorie della Società Botanica Italiana, Firenze.
- Öst. Bot. Zs., Wien*: Österreichische Botanische Zeitschrift. Wien.
- Pharm. J., London*: Pharmaceutical Journal and Transactions. London.
- Proc. Amer. Ass. Adv. Sci., Salem*: Proceedings of the American Association for the Advancement of Science. Salem.
- Schr. natw. Ver., Wernigerode*: Schriften herausg. vom naturwiss. Verein des Harzes. Wernigerode.
- Termt. Közl., Buda-Pest*: Természettudományi Közlöny. Buda-Pest. (Organ of the Royal Hungarian Society of Nat. Sc.)
- Verh. bot. Ver., Berlin*: Verh. d. botan. Vereins der Provinz Brandenburg. Berlin.

¹ The abbreviations for periodicals adopted in this translation are those employed in 'The International Catalogue of Scientific Literature. List of Journals and Supplementary ditto.' London, 1903 and 1904.—Tr.

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PREFATORY NOTE TO THE ENGLISH EDITION

THE scope of this book on Flower Pollination is so fully explained in the Author's Preface that little need be said by way of Preface to the Translation here presented. Müller's book upon the Fertilization of Flowers, upon which it is based, has been long out of print in English dress, and its place will now be taken by this encyclopaedic work of Knuth.

The present volume is the first of three comprising the work. It is general and deals with the structure of Flowers and of Insects in relation to Pollination.

The second volume, now in the press, is special and contains an account of all known observations upon the pollination of the flowers of plants of Arctic and Temperate zones.

The third volume, published, after the death of Knuth, under the editorship of Dr. Loew, deals similarly with plants from countries outside Europe.

In this English edition, the appendices of supplementary information in the original, inseparable from a work published by instalments during some years, will be incorporated in the body of the text, and this first volume contains a noteworthy feature in the Bibliography which includes, combined in one list, all the citations in the original and brings the record—notwithstanding the statements on page viii of the Author's Preface—down to Jan. 1, 1904. The adjustment of this list has been no easy task. The co-operation of Mr. J. M. F. Drummond of Cambridge and of Mr. S. A. Skan of Kew has been enlisted for the clearing up of some difficult points. The burden of revising the references, and of securing uniformity in and of checking the citations has been undertaken by Dr. Fritsch, and it is hoped that the care he has bestowed upon this feature of the volume will make the work more serviceable to readers.

It remains to state that the translation was begun primarily by Dr. Gregg Wilson. He had accomplished a considerable portion of his task when a call to the Professorship of Natural History in Queen's College, Belfast compelled him to seek relief from it. The Delegates of the University Press were fortunate in being able to entrust the continuance of the translation to the competent hands of Professor Ainsworth Davis of Aberystwyth, who, using as a basis Dr. Gregg Wilson's work, so far as completed, has given the translation the impress of his own qualities.

I. B. B.

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INTRODUCTION

FIRST SECTION

HISTORICAL DEVELOPMENT OF FLOWER POLLINATION¹

DR. JOSEPH GOTTLIEB KÖLREUTER² was the first to make observations on Flower Pollination and to expressly point out that the visits of insects are necessary for the pollination of flowers. In his work, 'Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen³' (Leipzig, 1761), with continuation (1763), second continuation (1764), and third continuation (1766), he communicates the results of numerous hybridization experiments, and in connection with these, gives his observations on the pollination of flowers by the agency of insects. The first sentences on this subject occur on page 21 and subsequent pages of the 'Preliminary Notice.' As they will always be noteworthy in the history of flower pollination, they may find place here. After mentioning the fig-tree as the only example till then known of a plant requiring the help of insects for pollination, Kölreuter continues:—'Experience has taught me that this, which has long been asserted concerning the fig-tree, is true of many other plants, some of them very common. In all cucumber plants (Cucurbitaceae), in all sword-lilies (Iridaceae), and in not a few plants of the mallow order (Malvaceae), pollination of the female flowers and stigmas is effected only by insects. I was amazed when I made this discovery in one of those plants for the first time, and saw that Nature had left so important a matter as reproduction to a mere chance, to a fortunate accident. My amazement was gradually converted, however, after prolonged observation, to admiration of the means, at first sight casual, but in fact most sure, which the wise Creator employs to secure reproduction. It is true that every movement of these small insect servants of Nature makes it quite evident that when they visit flowers, they have no intention of discharging an office so important. But what does that matter? It is enough that they, without themselves knowing it, undertake

¹ A full account of the historical development of flower pollination is given by E. Loew in his excellent work, 'Einführung in die Blütenbiologie auf historischer Grundlage' (Berlin, 1895, 8°, 432 and xii pp.).

² According to Sachs ('History of Botany,' Eng. Ed., p. 406, note), Kölreuter was born at Sulz on the Neckar, and died in 1806 as Professor of Natural History in Karlsruhe, where he was also superintendent of the Botanic and Royal Gardens from 1768 to 1786. There he began his investigations, which were subsequently continued in his own small garden, after he had given up his post, on account of the opposition of the gardeners.

³ This work has been republished by W. Pfeffer. It appeared in Ostwald's 'Klassiker der exakten Naturwissenschaften,' XLI (Leipzig, 1893).

most important work both for themselves and for the plants. Their needed sustenance, little drops of a sweet nectar, is hidden away down in these flowers. It costs them some trouble and labour to collect it; and during their manifold movements it comes about that they gather pollen in great quantity among the hairs of their body, to which it readily adheres, and rub it off again on the stigmas. As the surface of these is covered with innumerable warts, tubes, or spines, and smeared with an oily moisture, the pollen adheres more readily than to other parts of the flower. The insects, moreover, put pollen on the stigmas in a quantity far exceeding what is sufficient for complete fertilization; and this they do in so many flowers that Nature perfectly achieves her purpose. It will now be understood how it happens that cucumbers and melons will not prosper in hot-beds that are too well covered in. Until now, pollination of the female flowers has been ascribed to the wind, but other views would necessarily have prevailed if only close attention had been paid to the relative positions of the male and female flowers, to their forms, and to the character of the pollen. And how can one do this without at once recognizing in these busy insects the true agents of pollination? Certainly any one who had made these observations before me would have discovered this, and would have cleared up for himself and for all other Naturalists this secret of Nature. Whoever will convince himself of the truth of what I have here maintained with all caution, should give close attention throughout a whole day in still, clear, and warm weather (for then pollination is most commonly effected) to all that happens to one of the plants in question. He will then see that all manner of insects gradually assemble among the flowers, after these begin to open, that they wander about in them, and pass over from one to another. He will see that one after the other in the course of its manifold movements and turnings, gathers, on the hairy parts of its body, sometimes more, sometimes less of the pollen hanging on the stamens of a male flower, and soon thereafter either passes into another flower of the same kind, or goes into a female flower. In this latter case let him not disturb the insect, but await its voluntary departure, watching meanwhile at some distance all its movements. When it has gone, he should examine with a lens of low power the inner surface of the flower on all sides; and then pollen belonging to the same plant, and of which previously there was not a trace, will be found here and there adhering to the hairs of the flower, and especially to the stigma, which previously was quite free from it. This drama may often be seen re-enacted in the same blossom, so that the stigma about the time when the flower begins to close, will be almost completely covered with pollen. Occasionally, one may notice with satisfaction how a few of the insects roll about in the pollen, how they cover their whole body with it, and how, in this new golden costume they carry the fertilizing material in bulk to the female flowers.'

We find here a clear representation of cross-pollination by the help of insects, along with information as to the most favourable time for making observations. In the course of the memoir referred to, Kölreuter describes adaptations for pollination in several plants, e.g. in *Iris*, *Malva*, and *Viscum*; he also recognizes the dichogamy of *Polemonium*, *Oenothera*, and *Epilobium*. Referring to the flowers of the last-named plant (pp. 34 and 35), he says: 'The flowers of the willow-herb

(*Epilobium*, Linn. Sp. Pl., p. 347, notes 1 and 2) open before any of the anthers yield their pollen, before the pistil, which is curved downwards under the flower, begins to raise itself, and while the four stigmas still lie close together, before curving outwards and separating from one another, so as to expose their inner surfaces beset with little warts. . . . In the later flowers of this plant, pollination is effected entirely by insects, for the anthers open long before the stigmas become erect and spread out. Meanwhile, either the pollen is wasted on the anthers, or it is carried away by insects. So the stigmas remain without pollen, and no fertilization could occur unless insects were to bring fresh pollen from other flowers.' In connection with these observations, Kölreuter then dwells anew upon the importance of insects in fertilization:—'In general, plants in which pollination is not regularly effected by direct contact have the help of insects in effecting pollination, and consequently also fertilization. Probably the insects perform this very great service, if not for the majority of plants, at least for a very great number of them; since almost all such flowers as I refer to have something about them that is agreeable to insects, and it is not easy to find one about which these creatures do not swarm.'

If Kölreuter is to be regarded as the founder of flower pollination, we meet in Christian Konrad Sprengel¹ with a man who raised this branch of botany to a very high level, as he not only made clear the essential ideas of the theory of flowers, but also recorded an abundance of details with the most admirable acuteness. His work, '*Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen*' (Berlin, 1793, 4to), contains a description of floral adaptations in nearly 500 species of plants. Many of these are described in great detail, and with such accuracy that hardly anything can now be added, except information as to the visitors, with their scientific names; for Sprengel was an excellent botanist, but knew little about insects.

Seeing that Sprengel is so prominent in the history of flower pollination, it appears appropriate to give in his own words part of the introduction to his book. He begins as follows.—

'In the summer of 1787, while I carefully watched the flower of the wild geranium (*Geranium sylvaticum*), I found that the bases of its petals were provided on the inner side and on both edges with fine soft hairs. Convinced that the wise Creator of nature has brought forth not even a single hair without some particular design, I considered what purpose these hairs might serve. And here it occurred to me that if one starts with the supposition that the five drops of nectar, which are secreted from as many glands, are destined for the nourishment

¹ Christian K. Sprengel was born in 1750 at Brandenburg, and was the son of a clergyman. He studied theology and philology, and in 1774 became teacher at the school of the great Friedrichs-Hospital in Berlin. At the same time he gave instruction at the Royal *École Militaire*. In 1780 he became Rector at the great Lutheran School (the present Gymnasium) at Spandau. In 1794, after long struggles with his unfriendly superior, the Inspector-Superintendent Schulze, he was pensioned and retired to Berlin, where he died in complete seclusion on April 7, 1816. Further details as to the life of this great investigator occur in the following essays in the '*Naturwissenschaftliche Wochenschrift*,' viii (1893): 'Christian Konrad Sprengel, der Begründer der modernen Blumentheorie,' by O. Kirchner (Nos. 11 and 12), and 'Material zu einer Biographie Christian Konrad Sprengels,' by R. Mittmann (Nos. 13, 14, and 15).

of certain insects, one must at the same time find it not improbable that there should be some provision for preventing this nectar from being spoiled by rain, and that these hairs may have been placed here for the attainment of this purpose. . . . In the following summer I investigated the forget-me-not (*Myosotis palustris*). I found not only that this flower has nectar, but also that the nectar is completely protected against rain. At the same time, however, I was struck by the yellow ring, which surrounds the opening of the corolla tube, and which is so beautifully conspicuous



Fig. 1. Reduced title-page of Sprengel's book, taken from the edition edited by Knuth (in 'Klassiker der exakten Naturwissenschaften,' vols. xlviii-li).

against the sky-blue colour of the limb. Might not, I thought, this circumstance also have some reference to insects? Might not Nature have specially coloured this ring, to the end that it might show insects the way to the nectar reservoir? With this hypothesis in view, I examined other flowers, and found that most of them confirmed it. For I saw that flowers, in which part of the corolla is differently coloured from the rest, always have spots, figures, lines, or dots of peculiar hue just where the entrance to the nectar reservoir is situated. I now

inferred from the part to the whole. If, thought I, the corolla is coloured at one particular part specially for insects, then the whole colouring is for the benefit of insects; and if the particular colour of one part of a flower serves to enable an insect which has settled on the flower easily to find the right way to the nectar, then the general colour of the corolla is serviceable in rendering the flowers provided with it conspicuous even from afar to the eyes of insects that hover around in the air, in search of food.'

Even from these introductory words Sprengel's view of nature and his method, as well as his keen power of observation, and the clearness and simplicity of his mode of giving evidence may be recognized.

Connected with the above discoveries is the investigation in the summer of 1789 of a few species of *Iris*, from which Sprengel concludes that fertilization can only be effected with the help of insects. In the spring of the following year he remarked 'that *Orchis latifolia* and *Orchis Morio* have altogether the structure of nectar flowers, but do not contain any nectar.' Nevertheless 'these flowers are pollinated by certain flies which, deceived by their appearance, suppose that there is nectar in the spur, and accordingly creep in: but when they do this, they draw forth the pollen masses from their sacs, and carry them to the sticky stigmas¹. Flowers of this sort which have quite the appearance of nectar flowers, but do not contain nectar, I propose to call false nectar flowers.'

In the summer of the same year Sprengel discovered that in *Epilobium angustifolium* and in *Nigella arvensis* the stamens and carpels of one and the same flower do not develop simultaneously, a phenomenon he described as dichogamy; and when, in the spring of 1791, he found the 'female-male' (protogynous) dichogamy of *Euphorbia Cyparissias*, he was able to set forth his theory of flowers: 'In all those flowers which actually produce nectar, the following parts have to be distinguished':—

1. **The Nectary.** 'This is the part of a nectar flower which prepares and secretes the nectar.'

2. **The Nectar Reservoir.** 'This is the part of a nectar flower that receives and contains the nectar that is secreted by the nectary.'

3. **Parts protecting the nectar from rain: the Nectar Cover.** 'Nectar flowers are so constructed that insects can readily get to the nectar, but drops of rain, which fall on or into the flowers, always remain at some distance from the nectar, and so cannot mix with or destroy it².'

4. **Parts that enable insects readily to find the nectar: Corolla, Odour, Nectar Guides.** Nature 'has taken care that insects may recognize flowers even from afar, either by sight or by smell, or by both senses together. All nectar flowers are adorned with a corolla, and very many give forth an odour, which, as a rule, is pleasant to mankind, though frequently it is unpleasant, and occasionally

¹ Sprengel here overlooks the fact that the pollen masses are brought by the visiting insects, not to the stigma of the same flower, but to that of another (cf. my edition of Sprengel, I, p. 181).

² The 'nectar cover' of Sprengel protects the nectar in many cases, not so much from rain as from nectar-thieves.

intolerable ; but it is always agreeable to the insects for which the nectar is destined. The corolla is, except in a very few species, coloured, i. e. other than green, so that it is conspicuous against the green colour of the plants. Sometimes the calyx also is coloured, and when the corolla is developed, the calyx may be different from it, or if it makes one whole with this, it is similarly coloured on the inner side. But if the corolla is absent, then the calyx takes its place. . . . If now an insect, attracted by the beauty of the corolla, or by an agreeable odour, has gone to a flower, it will either forthwith perceive the nectar, or, if this is in a concealed place, will not perceive it. In the latter case Nature comes to the rescue with the nectar guide. This consists of one or several spots, lines, dots, or markings of another colour than that of the corolla as a whole, and consequently conspicuous against its lighter or darker tint. It is always placed just where the insects must creep in if they are to reach the nectar.'

'In connection with the nectar guide I must refer to the difference in nectar flowers with regard to the time of day at which they open. As there are insects that only move about in the daytime, so there are day flowers and night flowers. The day flowers burst forth into bloom in the morning. Many of them close in the evening, or incline downwards, while they stand erect by day. The day flowers are adorned with nectar marks, though not in all cases. The night flowers blossom in the evening. In the daytime most of them are closed or limp and inconspicuous, from which it is clear that they are not destined for day insects. The night flowers have a large and bright-coloured corolla, so that they are conspicuous to the eyes of insects in the darkness of the night. If their corolla is inconspicuous, the defect is made good by a powerful odour. No nectar guides occur in them ; for if the white corolla of a night flower had a nectar guide of another, but still light tint, this would not be conspicuous against the colour of the corolla in the darkness of the night, and so would be useless ; while if it had a dark-coloured nectar guide, this would be inconspicuous, and would therefore be as useless as the other.'

5. Pollination of nectar flowers by insects: Dichogamy. 'All these arrangements are in the first place and immediately for the benefit of insects, but through these also for the flowers themselves ; and their final purpose is that the flowers may be pollinated by insects. That insects play their part in the pollination of flowers has already been remarked by others. So far as I know, Kölreuter has gone furthest in this direction, as he discovered and clearly demonstrated the fact in *Iris*, for instance, and a few other genera. No one, however, has yet shown that the whole structure of nectar flowers points to this purpose, and can be fully explained with reference to it, for no one has recognized what I call the nectar cover and the nectar guide to be what they are, though every one has seen them. . . . There is undeniable evidence of the pollination of flowers by insects in the arrangement discovered by me in very many hermaphrodite flowers, which secures that no individual may be fertilized by its own pollen, but only by pollen from another individual. . . . This arrangement I call the development of sexual parts (anther and stigma) at different times, or shortly, dichogamy. It consists in this: After the flower has opened, the filaments have or assume, either all together or one after the other, a definite position, in which their anthers open, and their pollen

is available for pollination. Meanwhile, however, the stigma is in a place remote from the anthers, and it is still small and closed. Accordingly the pollen of the anthers can hardly, either by mechanical means or by an insect, be brought to the stigma, which does not yet exist. This condition endures for a definite time. After expiry of this, when the anthers have no more pollen, various changes in the filaments come about, and the result of these is that the anthers no longer occupy the place which they previously had. Meanwhile the pistil has so changed that the stigma is now exactly at the place where the anthers were at first; and as it opens, or the parts which compose it spread out, it takes almost exactly the position which the anthers formerly occupied. But it cannot now receive any pollen from the anthers, for they have none left. However, the point where at first the opening anthers and afterwards the opening stigma is found is so chosen in every plant that the insect for which the flower is adapted can only reach the nectar when it simultaneously touches the anthers of the younger flower, or the stigma of the older, with the same part of its body, thus removing pollen from the former and bringing it to the latter, and so pollinating the older flower with the pollen of the younger. These dichogamous hermaphrodite flowers are accordingly, so far as fertilization is concerned, like flowers with sexes half separated. At first they are male and afterwards female. . . . It never occurred to me whether the opposite of this arrangement might be found in Nature, whether there might be flowers whose stigmas ripened first, and whose stamens only began to mature after fertilization of the carpels. Though it was natural to come upon this idea, yet it did not occur to me till Nature itself brought me to it; and this occurred when I investigated *Euphorbia Cyparissias*. I saw there that as soon as a flower opens the stigmas first of all come forth, stand quite erect, and spread out. After a few days the whole pistil, which is upon a little stalk of its own, projects quite out of the flower, gradually losing the erect position, and finally turning its stigmas towards the earth. Only then do the stamens make their appearance one by one and the anthers take the same position which the stigmas formerly had.' Consequently if insects 'visit an older flower, they must necessarily carry off pollen from the anthers; and in order that they may do this unhindered, the pistil has left its former position and turned towards the earth. If the insects next visit a younger flower, they must pollinate the stigmas by touching them with their pollen-covered bodies, and so fertilize the younger flower with the pollen of the older.'

'As there are two kinds of dichogamy, they must be distinguished from one another by different names. The first discovered I call the male-female [we now say protandrous], and the later discovered the female-male [protogynous] dichogamy (*dichogamia androgyna*, *dichogamia gynandra*). The opposite of dichogamy is called homogamy.'

In contrast to nectar flowers, which are pollinated by the agency of insects, are flowers pollinated 'in a mechanical way by the wind.' These, the wind flowers as we now call them, produce a much greater quantity of pollen than the insect flowers. In the former there must be far more pollen than is required for fertilization, 'for the wind does not always blow it exactly towards the female tree, and moreover, does not bring every pollen-grain to a flower that has not been fertilized. Again, the rain not only washes much pollen from the anthers, but carries down

that which has been blown away, and is drifting in the air.' This pollen 'is very buoyant, and is readily carried away by the slightest breath of wind.' 'Both the anthers and the stigmas must be exposed to the air, so that the wind may carry the pollen from the former to the latter, and the stigmas must be a considerable size, because if very small they would but rarely receive pollen.'

Sprengel thus set forth the main ideas of flower pollination, and laid a foundation which was not to be built upon till two generations later. His investigations received little attention, or were made light of, and then passed wholly into oblivion, because of the influence of Linnaeus and his successors, who regarded the building up of systematic botany, the description of species, as the real end of botany. It was only on the appearance of Charles Darwin's¹ work on the Origin of Species (1859) that flower pollination came into prominence, and that Sprengel's work received due recognition².

It is true that Sprengel came very near understanding the use of cross-pollination for plants; but he does not express it. He is content to establish the fact of crossing, and to add the remark: 'As very many flowers are of separate sexes, and probably quite as many of the hermaphrodite ones are dichogamous, it seems that Nature is unwilling that any flower should be fertilized by its own pollen' ('Entd. Geh.,' p. 43).

Thomas Andrew Knight took a step further in the interpretation of these phenomena³. As early as 1799 he based upon the results of cross-fertilizations of cultivated plants the conclusion that *no plant fertilizes itself through many generations*.

In 1858 Darwin proved that in certain Papilionaceae, which he protected from visits of insects in Sprengel's way by means of a net, the formation of seeds is not so vigorous as when there is cross-fertilization. Darwin's work on the

¹ Charles Robert Darwin was born at Shrewsbury on February 12, 1809. In 1825 he entered the University of Edinburgh; he completed his studies at Cambridge, where he graduated in 1831. Subsequently he accompanied the expedition of Captain Fitzroy in the capacity of naturalist; visited Brazil, the west coast of South America, and the islands of the Pacific. In 1842 he inherited the property of Down near Beckenham, where he devoted himself to his studies till his death (April 19, 1882).

² In 'Nature,' xxix, H. A. Hagen opposes the current view that Ch. K. Sprengel's work had remained wholly unknown till brought to light again by Charles Darwin. He makes out that at least in Germany Sprengel's discoveries were well known to every naturalist throughout the century, and that between 1830 and 1840 Sprengel's doctrines were taught at every Prussian University. Fritz Müller (op. cit.) disputed Hagen's contention because he himself had heard hardly a word about Sprengel from Lichtenstein, or Knuth, or Erichson at Berlin in 1841, or from Hornschuch at Greifswald in 1842; and moreover his brother Hermann had heard nothing of Sprengel in Halle in 1848. K. Möbius (op. cit.) heard Schultz-Schultzenstein discuss Sprengel's theories in Berlin in 1850. H. A. Hagen (op. cit.) remarks that the well-known Berlin physician E. L. Heim discusses Sprengel's doctrines in spirited fashion in his diary, and states from personal recollection that Sprengel's discoveries were known in Berlin to Linde, Lichtenstein, Klug, and Erichson, in Bonn to Treviranus, in Breslau to Nees von Esebeck. Also according to him these doctrines were not forgotten in England, for Sprengel's views are considered in all of the seven editions of Kirby and Spence's 'Introduction to Entomology' that appeared between 1815 and 1867, the last issue comprising 13,000 copies. (From Koehne in Bot. Jahrb., Leipzig, i, 1885, pp. 731, 732.)

³ Knight (1758-1838) was for many years President of the Horticultural Society of London. See Ostwald's 'Klassiker,' No. lxii, which include six treatises by Knight on plant physiology.

significance of dimorphism appeared in 1862 (though the phenomenon had previously been observed by Sprengel, and even before him by Curtis, about 1780, see footnote, p. 45). In this work Darwin showed that the most abundant formation of seeds takes place when there is pollination of the stigmas with pollen from stamens standing at the same level in other flowers (legitimate fertilization). In the same year appeared his work on Orchids, in which he described the adaptations for fertilization of British and foreign orchids in as instructive a way as Sprengel (whose book was first again made mention of in this work, and so rescued from oblivion) had done in the case of numerous other plants seventy years previously. These investigations on orchids led to the conclusion that *Nature tells us in the most emphatic manner that she abhors perpetual self-fertilization*. Darwin found here, therefore, confirmation of the conclusion stated by him as a general law in his work on the Origin of Species—*No organic being can fertilize itself through an unlimited number of generations; but a cross with other individuals is occasionally—perhaps at very long intervals—indispensable*¹.

Although Darwin's first works on flower pollination were met with opposition, even by prominent botanists like L. C. Treviranus and H. v. Mohl, yet they had in a high degree a stimulating effect on numerous investigators, so that in the next few years there were not only various supplementary works published by Darwin himself (on *Linum*, *Lythrum*, *Primula*, &c.), but the science of flower pollination was added to by others and especially by German botanists. Thus, in the sixties, Alefeld, Hildebrand, Kuhn, Scott, and Walz worked at Heterostyly, while for descriptions published during this decade on the flower pollination of definite species or groups of plants we are indebted to Asa Gray, Anderson, Gosse, Scudder, Trimen, Weale, Crüger, Scott, Moggridge, Hildebrand, Hermann Müller, and Rohrbach on Orchids; to Robert Brown, Delpino, Hildebrand on Asclepiads and related forms; to Hildebrand who also worked on *Polygala*, *Salvia*, *Aristolochia*, and others; to Buchenau on *Pinguicula*, *Utricularia*, *Aspidistra*; to Fritz Müller on *Martha*; to Engler on *Saxifraga*.

In North America Asa Gray², after the appearance of Darwin's epoch-making works, made investigation in flower pollination, especially in North American orchids (*Platanthera*, *Gymnadenia*, *Goodyera*, *Spiranthes*), and subsequently on cleistogamy, self-fertility, humming-bird-flowers, and other special floral adaptations (1862).

In South America Fritz Müller³ followed in the steps of Darwin, publishing

¹ It may here be remarked that two more recent observations are opposed to this conclusion with regard to the avoidance of self-fertilization, namely:—(1) The flowers discovered by Burck of species of the tropical genera *Myrmecodia*, *Unona*, *Artobotrys*, *Goniolhamus*, *Cyathocalyx*, always remain completely closed. (2) The observation of Nathorst communicated by Aurivillius that the flowers of *Pedicularis lanata* (and *hirsuta*) in Spitzbergen, where it is reported that there are no humble-bees, produce fruit abundantly, and multiply by seeds, despite the fact that the anthers are so completely enclosed by the upper lip that only humble-bees are able to put in motion the mechanism of the flowers, and to effect a normal cross-fertilization. Accordingly it seems to be established that in these two cases self-fertilization has taken place through many generations and this without influence on the production of seed and the vitality of the offspring.

² Asa Gray was born on November 18, 1810, at Paris, in Oneida-County, in the State of New York. He first studied Medicine, but subsequently devoted himself to Botany, and in 1842 became Professor in Harvard College, Cambridge (Mass.). He died in this office on January 31, 1888.

³ For the following statement I am indebted to Professor F. Ludwig, of Greiz. Fritz Müller,

numerous admirable works on flower pollination, e.g. on adaptations for securing pollination in *Posoqueria* (1866) and *Heeria*, on humming-bird-flowers, on a poison-like action of pollen in cases of self-pollination, and on di- and tri-morphous plants of Brazil.

The individual investigations contained in numerous different periodicals made it necessary to collate and group the results. This was first done in the work

born on March 31, 1822, was the eldest son of Pastor Müller, Windischholzhausen, who was afterwards removed to Mühlberg, near Gotha. His mother was a daughter of J. Barth. Tromsdorf, the chemist of Erfurt. Fritz Müller, along with his brother Hermann, first attended the village school at Mühlberg under Rector Tanzer, and was afterwards prepared by his father for the gymnasium. In Erfurt he entered the third class, and there he passed the leaving examination. Thereafter, he prepared at Naumburg for the study of Pharmacy; but from 1840 onwards, he studied Natural Sciences and Mathematics in Berlin and Greifswald. After passing his examination as teacher, he spent his probation year at the gymnasium in Erfurt. With a view to making expeditions to foreign parts, he next studied Medicine, in the hope of becoming a naval surgeon. In 1852 he emigrated to South America. First he settled in Blumenau as a farmer, and afterwards went to the Lyceum in Desterro.

To this period belong his chief studies on marine animals (*Crustacea*). In 1864 his work 'Für Darwin' appeared. In 1865, after being driven by the Jesuits from his office, he returned to Blumenau as travelling naturalist of the province of Santa Catharina, and there he remained till the end of his life on May 21, 1897.

To this period also belong the following events of importance in his career:—

In 1884 (September): journey to the sea with his step-brother, Karl Müller, Professor of Zoology in Greifswald, who returned to Germany in June, 1885.

In 1885 he became acquainted with Eichler's Blütendiagramme, on the plan of which he worked through the Brazilian flora.

In 1886 he reported on excursions which he made with E. Ule; then he spent two memorable months with the German scientists Schimper and Schenck, who remained till November 11. To this time belong his chief investigations on figs, and fig-wasps.

In 1888 he received from Dr. Alfred Möller (assistant to Prof. Brefeld, in Münster), his work on the culture of Lichen-forming Ascomycetes without Algae; and to his joy recognized a nephew in the author. By this work, and also stimulated by E. Fischer (Phalloideae) and F. Ludwig, he was led to procure and study De Bary's 'Morphologie und Biologie der Pilze.'

In 1889 he was introduced by Ludwig to the writings of Brefeld, and later he received from Brefeld a treatise, and soon adopted his views on Mycology.

In 1889 the Brazilian Revolution broke out, and came to a temporary end on the expulsion of Dom Pedro, his friend and patron.

To the year 1890 belongs the visit of Alfred Möller, subsequently head-forester in Idstein, near Wiesbaden, and now Professor at the Academy of Forestry in Eberswalde. As Schimper and Schenck, under F. Müller's guidance, took back valuable treasures for German science (ant-plants, tropical epiphytes, and the like), so, under his uncle's superintendence, Möller's works on Hymenolichenes, Brazilian fungus-flowers, and fungus gardens of South American ants, &c., were produced.

Affairs in Brazil went from bad to worse. The new Government intimated to him without explanation that he was removed from his office and would receive no more pay. The album that was sent to him by German naturalists for his seventieth birthday reached him only on October 5, 1892. Letters were frequently not delivered at all at his address. In 1893 there was a battle in the neighbourhood of Blumenau. The revolutionaries robbed him of part of his property, and imprisoned him for eight days, and he was indebted for the preservation of his life only to a fortunate accident.

In 1894 his wife died on her 68th birthday. Two of his six daughters are married in Blumenau, one of them in Buenos Ayres. His grandchildren, Fritz and Hans Lorenz, are naturalists. They possess keen powers of observation and a warm interest in natural processes, like their grandfather, whom Charles Darwin justly named a 'prince of observers.' In the Bot. Centralblatt, lxxi, there appeared a full biography of Fritz Müller from the pen of F. Ludwig.

of Friedrich Hildebrand¹, which appeared in 1867: 'Die Geschlechtsverteilung bei den Pflanzen.' In this (pp. 72, 80) Hildebrand gave a classification of the floral arrangements known up to his time, as shown in the following summary:—

A. Male and female organs separate and in different flowers (**dicliny**); cross-pollination by wind or insects necessary (*Cannabis*).

B. Male and female organs in the same flower (**monocliny**).

I. The two sexes developed successively (**dichogamy**); self-pollination prevented in nature; cross-pollination by insects or wind.

(a) The male sex matured before the female (*protandrous dichogamy*; *Geranium pratense*).

(b) The female matured before the male (*protogynous dichogamy*; *Luzula pilosa*).

II. Both sexes developed at the same time (**adichogamy**).

(a) Flowers that open (*chasmogamy*, according to Axell).

1. *Anthems remote from the stigma*.

(a) The proportion between the length of the style and the length of the filaments varies in different plants of the same species (*heterostyly*); self-pollination is not prevented, but is either entirely without result (*Pulmonaria officinalis*), or is only slightly productive (*Primula sinensis*).

a. Two forms of flowers (dimorphism, Darwin).

β. Three forms of flowers (trimorphism, Darwin).

(b) The proportion between the length of the style and the length of the filaments is the same in all flowers (*homostyly*).

a. Sexual organs vary during the period of flowering as to their relative positions (*motion-dichogamy*); self-pollination avoided; cross-pollination by insects favoured (*Anoda hastata*, *Salvia*, &c.).

β. Sexual organs occupy the same relative positions throughout the period of flowering.

(a) Insect-help essential for pollination.

* Cross-pollination necessary; self-pollination by insects impossible, or at least very difficult (*Orchids*).

** Cross-pollination possible; self-pollination to some extent possible, but not necessary (*Asclepiadaceae*).

(β) Insect-help not essential for pollination; self-pollination possible, but cross-pollination by insects also occurs (*Vitis*, *Convallaria*).

2. *Anthems applied to the stigma, self-pollination therefore inevitable*.

(a) Fruit not forming without cross-pollination, which is possible only through the agency of insects (*Corydalis cava*).

(b) Formation of fruit even without cross-pollination; cross-pollination by insects not however excluded (*Linum usitatissimum*).

(b) Flowers that never open (*cleistogamy*, Kuhn); only self-pollination possible, cross-pollination excluded. In addition to these cleistogamous flowers the plant possesses others that open, and accordingly are liable to cross-pollination (*Oxalis Acetosella*).

¹ Professor in Freiburg i. B.

Hildebrand summarizes the results of his investigations in the following sentences (pp. 81, 82):—

1. The arrangements in most flowers are of such a kind that there is no self-pollination, but transference of the pollen from flower to flower is effected.
2. For this transference insects are in most cases necessary.
3. The prevention of self-pollination necessarily implies the prevention of self-fertilization.
4. In cases in which self-pollination is possible, or even inevitable, the possibility of cross-pollination is usually not excluded.
5. In these cases, also, insects are active agents for effecting cross-pollination.
6. There are probably no flowering plants in which cross-pollination is not possible, at least in some of the flowers, and in which constant self-pollination alone is possible; and therefore there are probably no flowering plants which furnish proof against the law that continuous self-pollination and self-fertilization are avoided.
7. Experiments have shown that in certain cases in which self-pollination was inevitable, or was artificially effected, there was nevertheless no self-fertilization; or if this did occur, the production of seed was less abundant than with cross-fertilization—a fact that agrees with the law to which reference has just been made.

8. A progressive series may be made out, starting from cases in which self-pollination and therefore self-fertilization are absolutely impossible, and leading to those in which it is possible, or even actually takes place, but in which the possibility of cross-pollination is not excluded.

9. The mode of distribution of the sexes and the kind of fertilization do not always agree in flowers that show morphological relationship. In certain families all the species are alike in sexual relations; but there are other families, or even genera, of which the species differ from one another altogether in this respect. Sexual relationships, accordingly, have not developed at the same rate and in the same way as morphological relationships, in the course of the metamorphosis and development of the flowering plants.

Hildebrand in his work gives to the Knight-Darwin law a somewhat different meaning, for he says (p. 5): *There are no sexual plants which can constantly reproduce themselves by self-fertilization alone; cross-fertilization is possible in all; in most cases self-fertilization is prevented by special adaptations, or is impossible, or at least is not advantageous, while cross-fertilization alone can occur, does actually occur, or has good results.*

Two years later (in 1869) Severin Axell¹ published a work 'Om anordningarna för de fanerogama växternas befruktning.' In this he gave a summary of floral

¹ According to information received by me from Professor A. G. Nathorst, of Stockholm, Johann Severin Axell was born on October 22, 1843; was a student in Upsala in 1861, and became Doctor of Philosophy and 'Docent' there in 1869. In 1868 he published in the 'Bot. Notisar' a treatise 'Om det färgade hyllets betydelse för växten,' and afterwards, in 1869, published as his degree thesis on taking the doctorate, the above-named work 'Om anordningarna för de fanerogama växternas befruktning.' He soon, however, gave up his scientific career on the death of his father, whose business as a timber-merchant in Sundsvall he took over. Subsequently he became a member of the Swedish Reichstag, and died at Wiesbaden on January 1, 1892.

arrangements, so far as he had recognized them in the flora of Sweden. This work is noteworthy, especially because the attempt is made 'to arrange all the floral adaptations of Phanerogams in a series, according to their natural development from the less perfect to the more perfect.'

It is remarkable that Axell doubts the occurrence of protogyny in insect-pollinated flowers, holding that in these only protandrous dichogamy is possible¹. On account of this belief, which is contrary to the facts, Axell does not give to protogyny a position of equal importance to protandry, and he is led to doubt the correctness of numerous observations that are opposed to his views. Axell introduces the term 'chasmogamy' as the contrary to cleistogamy; and by 'herkogamy' he understands a floral arrangement of such a nature that self-pollination—'homocliny' in contrast to 'heterocliny'—is impossible on account of the relative positions of stigmas and anthers.

At the close of the first part of his work, Axell gives the following summary (according to Loew's 'Einführung,' p. 152):—

Phanerogamous Flowers.

Heteroclinous Pollination.

Homoclinous Pollination.

A. <i>Hermaphrodite Flowers</i>			
impossible	I. Cleistogamous		necessary
	II. Chasmogamous		
possible	not necessary	co-ordinate with homoclinous pollination	(a) Homostylous
			(a) Mature stigmas surrounded by pollen of same flower
			(β) Mature stigmas not surrounded by pollen of same flower
			(b) Heterostylous
			(c) Dichogamous
necessary		favoured	(d) Herkogamous
			B. <i>Unisexual Flowers</i>
			impossible

Axell distinguishes the following oecological groups (Loew, op. cit., p. 152):—

A. Flowers which are pollinated with the help of an external agent. (**Chasmogamous flowers.**)

- I. Wind-pollinated. (*Anemophilous.*)
- II. Insect-pollinated. (*Entomophilous.*)

¹ Axell starts from the quite unfounded supposition that the corolla generally fades and secretion of nectar ceases as soon as pollen gets on to the stigma, and passes to the equally erroneous conclusion that in insect-pollinated flowers only protandrous dichogamy is possible. (Hermann Müller, 'Fertilisation,' Eng. Ed., p. 20, note.)

(a) Homoclinous pollination is prevented:

1. By dicliny: for each pollination two visits of an insect are necessary.
2. By dichogamy: for each pollination two visits of an insect are necessary.
3. By herkogamy: for each pollination a single visit of an insect is enough, inasmuch as in visiting such flowers the insect brings pollen to the stigma, and simultaneously carries away pollen to another flower.

(b) Homoclinous pollination is not hindered. For each pollination a single visit of an insect suffices.

1. Heterostyly.
2. Homostyly.

B. Flowers that are pollinated without the help of an external agent. (**Cleistogamous flowers.**)

Loew (op. cit., p. 153) gives the conclusions of Axell as follows:—Phanerogams are normally provided with open (chasmogamous) flowers, which can accordingly be crossed with those of other individuals. The active agents in the process are wind and insects. When the possibility of fertilization with foreign pollen is excluded, the phanerogams have flowers which do not open (cleistogamous flowers). They then fertilize themselves within the closed floral envelope. Among chasmogamous flowers homoclinous pollination is sometimes impossible (dicliny), sometimes prevented (dicho- and herkogamy), sometimes impeded (heterostyly), sometimes not impeded (homostyly): heteroclinous pollination is possible in equal degree in all. *Pollen from another flower surpasses in fertilizing effect pollen belonging to the same flower*, and crossing is accordingly the common mode of sexual reproduction in all cases. Fertilization with foreign pollen is also more advantageous than fertilization with pollen of the same plant. Plants whose sexual reproduction is better assured and in which it is effected with a greater economy of material, space, and time, are regarded by us as higher in respect to sexual propagation. The security of sexual propagation is greater as we pass from wind-pollinated to insect-pollinated plants. In anemophilous plants we find gradations from dioecism to monoecism and to protogyny: in entomophilous plants from dioecism to monoecism, protandry, herkogamy, heterostyly, and homostyly. The economy of material, space, and time increases in the same order. We see therefore that *the development of the arrangements for sexual union among the phanerogams has been and still is in this direction.*

In his work, 'Later observations on Dichogamy in the vegetable kingdom'¹ (Part I, 1868, 1869; Part II, fasc. 1, 1870; fasc. 2, 1875. Atti Soc. ital. sc. nat., Milano, xi, xii, and xvi), Federico Delpino² endeavoured with much success to arrange the previously known types of floral arrangement into oecological groups, and to set forth the relationships, so far as regards flower pollination, of kindred families. The classification of adaptations for pollination throughout the whole plant kingdom set forth by Delpino is still of value in some respects. It is therefore given in the second section of this volume.

Delpino was perhaps less fortunate in his attempt to refer all floral forms to a number of types, of which he distinguished 47, grouped into 13 classes.

¹ 'Ulteriori osservazioni sulla dicogamia nel regno vegetale.'

² Professor in Naples, and till 1893 in Bologna.

Class I. Arrangements for temporary imprisonment. (Apparecchi a carcere temporaria.) The visitors fall into a cavity, and remain for a time in captivity.

1. Aristolochia type.

(a) *Micromyophilous form*: Aristolochia Clematidis, pallida, rotunda, altissima, ciliata, Siphon, tomentosa, and saccata; Ceropegia elegans, Riocreuxia torulosa, Heterotropa asaroides, Asarum elegans, Thismia Brunoniania and clandestina, Arum italicum and maculatum.

(b) *Sapromyophilous form*: Aristolochia cymbifera, grandiflora, foetens, gigantea, and cordiflora; Sapria Himalayana, Hydnora africana and americana, Arisaema ringens; Arum crinitum, muscivorum, and Dracunculus.

2. Cyripedium type.

Cyripedium Calceolus and barbatum, Selenipedium caudatum.

3. Coryanthes type. (Perhaps both ornithophilous and mellitophilous.)

Coryanthes macrantha, Stanhopea grandiflora, Gloxinia maculata, Gongora speciosa, Eutoxeres Aquila.

Class II. Lodger arrangements. (Apparecchi a ricovero.) The visitors voluntarily spend some time in the flowers that protect them.

4. Aspidistra type.

(a) *Micromyophilous form*: Aspidistra elatior, Tupistra nutans, Ataccia cristata, Tacca integrifolia, Asarum europaeum and canadense, Ambrosinia Bassii, Atherurus ternatus, Arisarum vulgare and proboscideum.

(b) *Sapromyophilous form*: Rafflesia Arnoldi, Horsfieldi, Patma, &c.; Brughmansia Zippelii, Amorphophallus campanulatus, Dracontium polyphyllum, Simplicarpus foetidus, Arum triphyllum.

5. Magnolia type. (Beetle flowers.)

Magnolia grandiflora, &c., Nelumbium speciosum and luteum, Nymphaea alba, Victoria regia, Euryale ferox, Paeonia Moutan and albiflora, Calycanthus floridus, Eupomatia laurina.

6. Hydrangea type. (Beetle flowers.)

Hydrangea quercifolia, Cornus paniculata and sanguinea, Ligustrum vulgare, Fraxinus Ornus, Viburnum Opulus and Lantana; Sambucus nigra, Ebulus, and racemosa; Crataegus Oxyacantha, Ornithogalum arabicum.

7. Fig type.

Ficus Carica, Sycomorus, and others.

Class III. Tubular arrangements. (Apparecchi tubati.) The visitors enter the wide corolla tube, only remaining there long enough to gather pollen or suck nectar.

8. Datura type.

Datura arborea, sanguinea, and cornigera; Solandra laevis, Canna iridiflora, Fuchsia macrantha, corymbiflora, and fulgens. Cereus grandiflorus and others.

9. *Campanula* type.

Campanula Medium, *Trachelium*, *persicifolia*, and others; *Narcissus Pseudonarcissus*, *Colchicum autumnale*, *Crocus vernus*, *Gentiana acaulis*.

10. *Digitalis* type.

(a) *Sternotribous form*. (The pollen is carried by the visiting bees on their ventral surface.) *Cobaea scandens*, *Lisianthus acutangulus*.

(b) *Nototribous form*. (The pollen is carried by the visiting bees on their dorsal surface.) *Digitalis purpurea*, *Acanthus mollis* and *spinosus*, *Gladiolus segetum*, *Iris germanica* and *florentina*; *Serapias cordigera*, *longipetala*, and others.

Class IV. Pendulous arrangements. (*Apparecchi pendoloni*.) The visitors partly or entirely enter the pendulous flowers.

11. *Fuchsia* type.

Fuchsia coccinea and others, *Rigidella flammea*, *Ribes speciosum*.

12. *Abutilon* type.

Abutilon striatum and others, *Thibaudia bracteata*, *Clivia nobilis*, *Nicotiana Langsdorffii*; *Lachenalia pendula*, *tricolor*, and others.

Class V. Small-mouthed flowers. (*Apparecchi microstomi*.) Owing to the narrowness of the corolla, visitors can only introduce their sucking organs: frequently ornithophilous.

13. *Microstomous* type.

Tropaeolum tricolorum and others, *Siphocampylus microstoma*; *Erica cerinthoides*, *ampullacea*, *ventricosa*, *retorta*, and others.

Class VI. Labiate arrangements. (*Apparecchi labiati*.) Bilaterally symmetrical flowers with nectaries on the under side, while anthers and stigmas are on the upper side. Visitors (bees, birds) touch the anthers and stigmas with their backs.

14. *Labiate* type.

(a) *Galeate form*: *Galeopsis*, *Lamium*, *Justicia ventricosa*, *Ravenia spectabilis*, *Epipactis latifolia*, *Cephalanthera*, *Spiranthes*, *Conospermum taxifolium*, *Orobanche*, *Tozzia alpina*, *Erythrina Cristagalli*.

(b) *Ringent form*: *Aphelandra cristata* and *aurantiaca*, *Lallemantia canescens*, *Pedicularis*, *Rhinanthus major*; *Salvia officinalis*, *pratensis*, *glutinosa*, *Sclarea*, and others; *Curcuma cordata* and others.

(c) *Personate form*: *Antirrhinum*, *Linaria*, *Utricularia vulgaris*, *Rhynchoglossum zeylanicum*, *Calceolaria*.

(d) *Labiate form*: *Orchis*, *Listera ovata*, *Alpinia nutans*; *Balsamina impatiens*, *hortensis*, and others; *Pinguicula*.

(e) *Unilabiate form*: *Teucrium*, *Ajuga*, *Lobelia*.

15. *Aeschinanthus* type.

Aeschinanthus grandiflorus, *pulcher*, *Lobbianus*, and others; *Gesneria bulbosa*, *Tecoma capensis*, *Bignonia venusta*, *Epiphyllum truncatum*, *Ruellia macrophylla*, *Canna*, and others.

16. Violet type.

Viola canina, *odorata*, *tricolor*, and others; *Gratiola officinalis*, *Epipogum Gmelini*.

Class VII. Papilionaceous arrangements. (Apparecchi papilionacei.) The visitors touch the anthers and stigma of the bilaterally-symmetrical flowers with their ventral surface.

17. Normal papilionaceous type, with concealed anthers.

(a) *Common papilionaceous form*: *Robinia* and others, *Collinsia bicolor* and *verna*, *Polygala myrtifolia*, *Pelargonium rutaefolium*, *Pavia rubra*; *Corydalis cava*, *solida*, and others; *Dicentra*.

(b) *Tension form* (Forma a scatto): *Genista*, *Cytisus canariensis* and *albus*, *Ulex europaeus*; *Spartium junceum*, *scoparium*, and others; *Medicago*, *Indigofera*, *Desmodium*, *Maranta*, *Calathea*, *Schizanthus*, *Polygala mixta*, and others.

(c) *Pump form* (Forma a stantuffo): *Lotus*, *Bonjeanea*, *Tetragonolobus*, *Hippocrepis*, *Coronilla*, *Anthyllis*, *Lupinus*, *Ononis*, and others.

(d) *Brush form* (Forma tricotila): *Phaseolus*; *Vicia sativa*, *sepium*, *faba*, *Cracca*, and others; *Pisum sativum*, *Orobis*, *Lathyrus*.

18. Papilionaceous type with exposed stamens.

Ocymum basilicum, *Prostanthera*, *Delphinium*, *Aconitum*, *Tropaeolum majus*, *Cuphea viscosa* and others, *Aquilegia*.

19. Amaryllis or Rhododendron type.

(a) *Form with stamens completely or almost completely enclosed*: *Rhododendron arboreum*, *ferrugineum*, and *Nuttalli*; *Funkia lancifolia*, *Lilium longiflorum*, *Hemerocallis coerulea*; *Alstroemeria peregrina*, *pulchra*, and others; *Agapanthus umbellatus*; *Amaryllis formosissima*, *vittata*, *Reginae*, *equestris*, and others; *Pontederia azurea*.

(b) *Form with exerted stamens*: *Echium vulgare*, *Aesculus Hippocastanum*, *Dictamnus albus*, *Amherstia nobilis*; *Capparis acuminata*, and others.

20. Melastomaceous type.

Many *Melastomaceae*, *Solanum amazonicum*; *Cassia floribunda*, *Chamaecrista*, and others; *Physostemon*.

21. Strelitzia type.

Strelitzia Reginae and *Augusta*.

Class VIII. Narrow-tubed arrangements. (Apparecchi sifonifori e macrosifoni.) The corolla tubes are long, and often so narrow that only sphingidae can get at the honey.

22. Long-spurred type. (Tipo sifonopetalo.)

Gymnadenia conopsea and *albida*, *Linaria chalepensis*, *Anacamptis pyramidalis*, *Platanthera bifolia* and *chlorantha*; *Angraecum sesquipedale*, *caudatum*, and *apiculatum*; *Habenaria longicauda*, *macroceras*, *gigantea*, and *procera*; *Limodorum falcatum*, *Impatiens scapiflora*, *Pelargonium nocturnum* and *lobatum*.

23. Long-flowered type. (Tipo sifonante.)

Saponaria officinalis, *Lychnis vespertina* and *diurna*; *Lonicera Caprifolium*, *Periclymenum*, *sempervirens* and *longiflora*; *Pancratium maritimum* and *illyricum*, *Watsonia roseo-alba*, *Ruellia lilacina*; *Gladiolus tristis*, *cuspidatus*, and *angustus*; *Erinus lychnidea*, *Crinum*, *Pancratium*, species of *Gardenia*, *Portlandia grandiflora*, *Mirabilis Jalapa*, *Ipomoea Bona-nox*, *Nicotiana noctiflora* and *persica*, *Oenothera*, and others.

Class IX. Arrangements for hovering visitors. (Apparecchi circumvolatorii.) Sphingidae and birds effect pollination while hovering before the flower.

24. Methonica type.

Methonica superba, *Lilium Martagon*.

25. Stenocarpus type.

Stenocarpus Cunninghami, *Marcgravia*, *Passiflora princeps*.

26. Crocus type.

Lilium croceum.

27. Protea type.

Protea mellifera, *speciosa*, *acuminata*, *latifolia*, *longiflora*; *Haemanthus*, and others.

28. Callistemon type.

Callistemon, *Calothamnus*, *Metrosideros speciosa*, *Banksia*, *Dryandra*, and others.

Class X. Arrangements for wandering visitors. (Apparecchi perambulatorii.) The visitors (bees) wander about, either on the whole surface to be pollinated, or only on a ring-like zone of it.

29. Passiflora type.

Passiflora coerulea, *Napoleona imperialis*.

30. Nigella type.

Nigella arvensis and *damascena*, *Swertia perennis*, *Helonias glaberrima* and *bracteata*.

31. Helianthus type.

Helianthus annuus, *perennis*, and *tuberosus*, and some other *Compositae*.

Class XI. Arrangements for creeping visitors. (Apparecchi reptatorii.) The visitors (snails) crawl about on the flat inflorescence.

32. Rhodea type.

Rhodea japonica, *Dracontium pertusum*.

33. Anthurium type.

Anthurium lanceolatum and *Scherzerianum*, *Dorstenia ceratosanthes* and *Houstoni*.

34. Chrysosplenium type.

Chrysosplenium alternifolium.

Class XII. Prehensile arrangements. (Apparecchi prensili.) The visitors grasp the style and stamens in such a way as to cover their breasts with pollen, and then effect cross-pollination.

35. **Borago type.**

Borago officinalis; *Cyclamen europaeum*, *coum*, *persicum*, and others; *Dodecatheon Meadia* and *integrifolium*; *Solanum Dulcamara*, *nigrum*, *tuberosum*, *Lycopersicum*, *insanum*, and others; *Verbascum Myconi*, *Galanthus nivalis*, *Leucojum vernum*, *Conanthera bifolia*, *Cajophora lateritia*, species of *Loasa*, *Sollya linearis*, *Dianella coerulea*, and others.

36. **Verbascum type.**

Verbascum, *Tradescantia virginica*, *Anagallis latifolia*, *Arthropodium paniculatum*, *Helianthemum*, *Chelidonium majus*, and others.

Class XIII. Regular open arrangements. (*Apparecchi aperti, regolari.*) The widely open flowers are visited by insects of the most varied kind (beetles, bees, flies, occasionally butterflies, &c.).

(a) *Green open arrangements* (*Apparecchi aperti, cloranti*).

37. **Rhamnus type.**

Rhamnus cathartica, *Frangula*, and others; *Euonymus europaeus*, *latifolius*, and *japonicus*; *Paliurus aculeatus*, species of *Rhus*, *Ilex Aquifolium* and *latifolium*; *Euphorbia sylvatica*, *amygdaloides*, and *dendroides*; *Hedera Helix*, *Buxus sempervirens*, *Ribes rubrum* and *alpinum*, the *Umbelliferae*.

(b) *Black open arrangements* (*Apparecchi aperti, melananti*).

38. **Uvaria type.**

Uvaria nicaraguensis, *Asimina triloba*, *Thottea grandiflora*.

39. **Stapelia type.**

Stapelia, *Boucerosia*, *Caralluma*.

40. **Dark type.**

Periploca graeca, *Microstemma*, *Cynanchum nigrum*, *Euonymus verrucosus*, *Aucuba japonica*, *Ruscus aculeatus*, *Streptopus amplexifolius*, and others.

(c) *Many-flowered open arrangements* (*Apparecchi aperti, polianti*).

41. **Stellate type.**

Many *Compositae*, *Actinotus Helianthi*; *Astrantia maxima*, *major*, *media*, and *minor*; species of *Bupleurum*, *Cupularia viscosa*.

42. **Scabious type.**

Scabiosa, *Cephalaria*, *Brunonia australis*, species of *Pimelea*, species of *Valeriana*, *Jasione montana*.

43. **Trachelium type.**

Trachelium coeruleum, *Centranthus ruber*.

(d) *Brightly coloured open arrangements* (*Apparecchi aperti, callipetali*).

44. **Papaver type.**

Papaver Rhoeas, *orientale*, *argemone*, and others; *Tulipa Gesneriana* and *Clusiana*, *Chelidonium glaucium*, *Cistus ladaniferus* and *formosus*, *Anemone hortensis* and *coronaria*.

45. **Rosa type.**

Rosa bengalensis, *damascena*, *canina*, *sempervirens* and others; *Camellia japonica*, and others.

46. *Ranunculus* type.

Ranunculus, *Eranthis*; *Anemone nemorosa*, *trifolia*, *Hepatica*, and *ranunculoides*; *Agrimonia*, *Fragaria*, *Rubus*, *Potentilla*, *Geum*; *Hypericum perforatum*, *humifusum*, *montanum*, and others; species of *Geranium* and *Erodium*; *Scilla bifolia* and *autumnalis*, and others.

(e) *Small-flowered open arrangements* (*Apparecchi aperti*, *brachipetali*).

47. *Small-flowered type*.

Many *Alsineae* (e. g. *Stellaria media*) and *Cruciferae* (e. g. *Capsella Bursa-pastoris*, *Erophila verna*), also *Veronica*, and so forth.

These types of Flower Pollination established by Delpino, have been received with a considerable amount of hostile criticism, especially by Hermann Müller ('*Weit. Beob.*, III, p. 20). This investigator describes them as to some extent quite arbitrary, 'It is obvious,' he says, 'that we cannot escape the unnatural, if we attempt to coerce the almost endless variety of floral forms into a definite number of sharply circumscribed types.' Delpino, for instance, mentions the sixth or *hydrangea* type as being specially adapted for *Cetonia* and other *lamellicorns*, and yet numerous species of this type are chiefly visited by flies, bees with short proboscides, and by butterflies. Again, Delpino adduces *Solanum Dulcamara* as a beautiful example of the *borage* type (*bella espressione del tipo*). With regard to this, Hermann Müller speaks in somewhat the following way (*op. cit.*, pp. 20-2): *Borage* is quite rightly regarded by Delpino as only adapted for pollination by bees, since bees alone are capable of clambering up from below into the downwardly turned flowers, and sinking the proboscis into the honey-bearing base of the blossom. It may also be correct that in all other flowers in which the anthers are borne upon short, stiff filaments, and enclose the conical style, bees are the necessary agents of cross-pollination. Delpino, however, does not content himself with establishing this, but brings together such varied flowers as *Borago*, *Cyclamen*, *Solanum*, *Galanthus*, *Leucojum*, and several foreign species under this one type. He explains away those instances where insects other than bees play an important part in crossing, as e. g. pollen-eating hover-flies in the case of our native species of *Solanum*, by affirming that their visits are purely accidental and without significance.

In contrast to this severe judgment of Hermann Müller's, E. Loew very properly contends ('*Einführung*,' p. 191) that the establishment and characterization of floral types by Delpino, must be regarded as one of the most suggestive and brilliant attempts towards the solution of a problem which, owing to its nature, must always remain open. Any hypothesis that may be advanced continually requires improvement and extension, according to the standpoint of science for the time being.

Moreover, Delpino speaks like Knight, Darwin, and Hildebrand as to the great law of *Dichogamy* or *Cross-fertilization* (*la gran legge della dicogamia o delle nozze incrociate*).

The work of Hermann Müller¹, '*Die Befruchtung der Blumen durch Insekten*

¹ Heinrich Ludwig Hermann Müller was born on September 23, 1829, at Mühlberg in Thuringia, and was the son of a minister (cf. the note on p. 9). In 1847 he attended the

und die gegenseitigen Anpassungen beider' (Leipzig, 1873), which meanwhile appeared, was of remarkable importance for the study of Flower Pollination. It was followed in 1881 by Müller's second great work, 'Alpenblumen,' and in 1878-1882 by his third—'Weitere Beobachtungen über die Befruchtung der Blumen durch Insekten.' These works embrace not only an amazing number of individual observations with reference both to the floral arrangements of many hundreds of plants and also to the visits of many thousands of insects, but they also furnish evidence for the floral theory established by the author. The principles enunciated by Knight, Darwin, Hildebrand, and Delpino offered no explanation of the numerous known instances of fruitful self-pollination, including cases of cleistogamy. For the one-sided 'Law' of the above-named investigators—a Law that was not universally proved,—Müller substituted the following statement, the *direct* proof of which rested on Darwin's experiments, while the *indirect* proof was based on the floral arrangements of plants in general, and, more particularly, on adaptations in the flowers themselves: *Whenever progeny resulting from crossing comes into serious conflict with the offspring resulting from self-fertilization, the former is victorious. Only where there is no such struggle for existence can self-fertilization often prove satisfactory for many generations.*

That direct and indirect proofs attest the correctness of this great law of life has already been stated. They are given as follows by Hermann Müller (in 'Alpenblumen,' pp. 474-5):—'In the flowers investigated in this connection, it appeared, as first shown at any length in 'Die Befruchtung der Blumen durch Insekten,' to be a general rule, offering only a few easily explained exceptions, that flowers to which insect visits are constant and sufficient, are adapted exclusively for crossing by the insects, and that, on the contrary, in proportion as insect visits are uncertain, the floral arrangements permit or favour spontaneous self-fertilization. It appears from the direct experiments of Darwin, as well as from the pollination

University of Halle to study Natural Science. He devoted himself here chiefly to Geology, to which he also applied himself enthusiastically in Berlin, during his stay there from 1849 to 1852. In 1852 he passed the Examination pro Facultate docendi and spent the following winter in the house of his parents. In 1853 he made his first journey to the Alps, this being chiefly undertaken in furtherance of his geological studies, though he also did something in the way of collecting plants and insects. From Michaelmas, 1853, till the following Michaelmas, Müller spent his year of probation in the Friedrich-Wilhelm Gymnasium at Berlin. Next winter he took the place of a teacher in Schwerin who was sick. His first journey in the Alps had aroused in him an appreciation for the rich flora and fauna of the Highlands, and in 1855 he undertook his second alpine journey, and this was specially devoted to Botany and Entomology. In the same year Müller was called to the Realschule in Lippstadt, which was then in course of formation. In 1856 he was definitely placed on the staff of this institution; in 1865 he became upper-master; and in 1883 he received the title of Professor.

The 'Origin of Species,' and Darwin's book on Orchids had so great an influence on Hermann Müller, that from 1866, the year in which he became acquainted with these works, he devoted his knowledge, his energy, and his power of research wholly to Pollination. In 1873 appeared his first great work, 'Die Befruchtung der Blumen durch Insekten'; in 1881 his second, 'Die Alpenblumen'; from 1878 to 1882 his third, which forms a completion to the first, 'Weitere Beobachtungen über die Befruchtung der Blumen durch Insekten.' Hermann Müller died on August 25, 1883, of pulmonary disease, while travelling in the Tyrol in pursuit of Science, and for the benefit of his health. A full account of his life, and of his services to Pedagogy, and more especially to Pollination, is given by F. Ludwig in the Bot. Centralbl., 1884, vol. xvii, pp. 393-414, under the title 'Das Leben und Wirken Professor Dr. Hermann Müller's.' See also E. Krause in the work, 'Hermann Müller von Lippstadt. Ein Gedenkblatt. Lippstadt, 1884.'

arrangements of flowers considered in relation to actual insect visits, that crossing is absolutely the more advantageous mode of fertilization. If, on the one hand, the experimental method has the advantage of being directly demonstrative, there^e is, on the other hand, a much larger amount of indirect evidence adducible from the arrangements for pollination. It is, perhaps, hardly more difficult to obtain indirect evidence from a few hundred flowers than to make direct experiments on a few. If by itself, such evidence would scarcely satisfy us, yet it brings complete conviction when considered along with the results of the Darwinian experiments, and takes us even a step further than those experiments. From Darwin's experiments, which lasted eleven years, it is not proved, and perhaps it would not be proved if the experiments lasted a hundred years, whether the capacity of certain flowers to reproduce by spontaneous self-pollination is limited or unlimited. From the floral arrangements, on the other hand, we can conclude that this capacity must have its limit. For, were it unlimited, cleistogamous flowers would be the most advantageous, and many plants would necessarily have come to possess such flowers only. As a matter of fact, however, not a single plant is known which reproduces itself exclusively by spontaneous self-fertilization. The investigation of pollination arrangements in connection with actual insect-visits therefore furnishes evidence that is very convincing, even though of secondary nature. It constitutes a no less essential support of the floral theory than the experimental proof that, as a matter of fact, more vigorous offspring result from crossing than from self-fertilization.'

Hermann Müller's works stimulated many botanists in the most marked way, and a vigour never before manifest became apparent in the field of Flower Pollination. In addition to the older specialists, Darwin, Delpino, Hildebrand, Hermann Müller, and his brother, who was no less enthusiastic for this science, a number of younger investigators began to apply themselves to this branch, so that a division of labour resulted, and the investigations undertaken in various districts were directed partly to the extension of the various sections of Flower Pollination, partly to an investigation of floral arrangements, and the discovering of the visitors of flowers. Our knowledge of nectaries¹ was extended in Germany by the works of W. J. Behrens; in France by Gaston Bonnier; in North America by Trelease (all 1879). Investigations on stamens were published by Chatin (France), Askenasy, H. Fischer, Oetker (Germany), Bennett (England); on stigmas by J. Reinke, Behrens (Germany), Capus (France); on the processes of fertilization by Dalmer, Strasburger, Elfving, Treub, Jurányi, Goroschankin, Guignard; on the distribution of sexes by Asa Gray, E. Warming, Hackel, Breitenbach, Magnus, Potonié, Errera and Gevaert, F. Ludwig, Solms-Laubach; on heterostyly by Breitenbach, Kny, Köhne, W. Burck, Urban, Bailey, Clarke, Meehan, Ernst, Bessey, Battandier, Todd, Knoblauch, Pirota, Wilson; on cleistogamy by Ascherson, Potonié, Batalin, Ludwig, Trelease, Heckel, Pringle, Asa Gray, Godron, Hackel, Meehan, Coulter, Graebner, Schröter, Battandier, G. M. Thompson, Grisebach, Drude, Kearney, Köhne, Solms-Laubach, Burck; on pseudo- and hemi-cleistogamy by Fitzgerald, Moore, Reichenbach fil., Freyhold,

¹ Partly taken from Loew:—'Einführung in die Blütenbiologie,' pp. 291 et seq., and 'Blütenbiologische Floristik,' pp. 172-5.

Eggers, Henslow, Meehan, Coulter, Bush, Battandier, Errera and Gevaert; on self-sterility by Gentry, Warming, Meehan, Delpino, Ludwig, Schneck, Rimpau, Liebenberg, Hoffmann, Neubert, Focke, Eggers, Hunger, Battandier; on self-fertility by Pedicino, Comes, Meehan, Caruel, Wilson, Henslow, Asa Gray, Delpino, Ludwig, Hoffmann; on the relations between crossing and self-fertilization by Henslow, Meehan, Pedicino, Caruel, Comes. Cultivation and pollination researches were carried out by Hoffmann, Wilson, Rimpau, Liebenberg, Beal, Vilmorin, Ottavi, Horváth.

Within a few years after the appearance of the first of Müller's works, Errera and Gevaert were able to publish a summary of the various arrangements for pollination known up to 1878, in their work 'Sur la structure et les modes de fécondation des fleurs' (Bul. Soc. roy. bot., Gand, xvii, 1878). Loew ('Einführung,' pp. 324-7) gives this summary as follows:—

I. MONOMORPHOUS INDIVIDUALS, i.e. in respect of flowers all the individuals are alike.

1. MONOMORPHOUS FLOWERS. All flowers alike, and hermaphrodite.

A. **Cleistogamy** (Kuhn). All the flowers remain permanently closed; crossing is impossible.

B. **Chasmogamy** (Axell). All flowers open; crossing is always possible.

(a) **Direct Autogamy**. The pollen falls directly on the stigma of the same flower.

a. *Direct Autocarpy*. Self-pollination is effective: *Trifolium arvense*.

β. *No direct Autocarpy*. Self-pollination is not effective: *Corydalis cava*.

(b) **No direct Autogamy**. The pollen does not fall directly on the stigma.

a. *Herkogamy* (Axell). The mature anthers and stigmas are remote from one another: *Anacamptis pyramidalis*.

β. *Dichogamy* (Sprengel). The anthers and stigmas are mature at different times.

* *Proterandry* (Delpino). The anthers open before the stigmas are ready for pollination: *Teucrium Scorodonia*.

** *Proterogyny* (Delpino). The stigmas are ready for pollination before the opening of the anthers: *Aristolochia Clematitis*.

2. PLEOMORPHOUS FLOWERS. The flowers of various individuals are different.

A. **Chasmo-Cleistogamy** (Delpino). The constantly hermaphrodite flowers differ from one another in the mode of pollination, some being cleistogamous, others chasmogamous: *Oxalis Acetosella*.

B. **Monoecism**. The flowers of the same stock differ from one another in sex: there are always a few flowers that are not hermaphrodite.

(a) **Dimonoecism**. The flowers of the same individual are of two kinds.

a. *Andromonoecism* (Darwin). Flowers hermaphrodite and male: *Veratrum album*.

β. *Gynomonoecism* (Darwin). Flowers hermaphrodite and female: *Parietaria officinalis*.

- γ. *Agamonoecism*. Flowers hermaphrodite and neuter: *Viburnum Opulus*.
- δ. *Monoecism* or *Androgyny proper* (Linnaeus). Flowers male and female: *Cucurbita Pepo*.

- (b) **Trimonoecism**. The flowers of the same individual are of three kinds. Monoecious polygamy (Darwin). Flowers hermaphrodite, male, and female: *Saponaria ocymoides*.

II. PLEOMORPHOUS INDIVIDUALS. There are different kinds of stocks distinguished by their flowers.

A. **Heteromesogamy**. The individuals differ from one another in the arrangements for the pollination of their flowers.

- (a) **Auto-allogamy**. Some individuals of a species are adapted for Autogamy: others for Allogamy: *Viola tricolor*.
- (b) **Homo-dichogamy** (Errera and Gevaert). Some individuals are homogamous; others are dichogamous: *Ajuga reptans*.
- (c) **Anemo-entomophily**. Some individuals are adapted for insect-pollination; others for wind-pollination: *Plantago media*.
- (d) **Di-entomophily**. One group of individuals is adapted for a definite class of insects; another group for a different class: *Iris Pseudacorus*, *Primula farinosa*.

B. **Heterostyly** (Hildebrand). The individuals are distinguished from one another by the remote position of the sexual organs; the union of two individuals of dissimilar form is necessary for complete fertility.

- (a) **Heterodistyly**. With two kinds of individual, some with long style others with short: *Primula elatior*.
- (b) **Heterotristyly**. With three kinds of individual, some flowers with long style, others with medium, others with short: *Lythrum Salicaria*.

C. **Hetero-dichogamy**. The individuals differ from one another in point of time, as regards the sequence of the ripening of their sexual organs: *Juglans regia*.

D. **Polyoecism**. The individuals differ from one another in sex.

- (a) **Dioecism**. The individuals are of two kinds.
 - α. *Androdioecism* (Darwin). In some individuals hermaphrodite flowers; in others male: *Dryas octopetala*.
 - β. *Gynodioecism* (Darwin). In some individuals hermaphrodite flowers; in others female: *Thymus Serpyllum*.
 - γ. *Dioecism proper* (Linnaeus). In some individuals male flowers; in others female: *Salix caprea*.
- (b) **Trioecism** or **Trioecious polygamy** (Darwin). Some individuals hermaphrodite, others male, and still others female: *Fraxinus excelsior*.

Through the investigations of Warming, Ludwig, Kirchner, Schulz, and Loew this arrangement was subsequently altered and extended to some extent.

The means by which flowers attract insects were studied by Grant Allen, and afterwards in a very exhaustive way by Hermann Müller ('Alpenblumen'). The

latter gives (op. cit.), moreover, a grouping of plants according to their floral arrangements, and seeks to establish by statistics, the connection between floral mechanisms and the bodily structure of the visitors. The floral statistics begun by Müller were later on extended by others, especially by Loew, MacLeod, and myself.

While many investigators busied themselves with the representation of general floral arrangements, a still larger number investigated the mechanisms for pollination in individual flowers, or groups of flowers. These researches, which have been carried out in all parts of the world, cannot possibly be even indicated here, and reference is therefore made to the bibliography.

It must be the aim of research in Flower Pollination to make out the adaptations of all flowers and their pollinators, and this end can only be approached if such investigations are systematically carried on¹ in as many small and clearly demarcated areas as possible. For the attainment of this end, it is necessary that numerous observers should take part in the work, and that the earth should be covered with a net-work of stations² for the study of flower pollination. As yet, but few attempts have been made in this direction. In the first place there must be mentioned, as standing far above all other attempts, the work of Hermann Müller ('Alpenblumen,' Leipzig, 1881), already referred to several times. It contains the observations of this genial and untiring author, made in the East Alps (especially in the Canton Graubünden) during the years 1874-9.

Of similar worth is MacLeod's book, 'De Pyreneeënbloemen en hare bevruchting door insecten' (Ghent, 1891). It contains investigations and observations in flower pollination made by MacLeod in the Pyrenees during the years 1889 and 1890.

The same investigator, in his work, 'Over de bevruchting der bloemen in het Kempisch gedeelte van Vlaanderen' (Ghent, 1893-4), gives an account of the floral arrangements of the plants of the Kempian part of Flanders, and enumerates many floral visitors.

O. Kirchner in his 'Flora von Stuttgart' (1888) describes the floral arrangements occurring in that neighbourhood, so far as known up to his time.

C. Verhoeff in his work, 'Blumen und Insekten der Insel Norderney' (Nova Acta d. Kais. Leop.-Carol. Deutschen Akad. der Naturf., lxi, 1893), gives an exhaustive account of the mutual relations existing between flowers and insects in that island.

My own memoirs on the same lines refer for the most part to the relations subsisting between flowers and their visitors on the islands in the German North Sea. A comprehensive work of this kind is 'Blumen und Insekten auf den nordfriesischen Inseln' (Kiel, 1895). This has been supplemented by my publications, 'Weitere Beobachtungen über Blumen und Insekten auf den nordfriesischen Inseln' (Kiel, 1895), 'Blumen und Insekten auf den Halligen' (Ghent, 1894), and 'Blumen und Insekten auf der Insel Helgoland' (Ghent, 1896). I further conducted a partially systematic investigation into flower pollination on the Island of Capri (1892), in Thuringia (1894), on the Island of Rügen (1896), and since 1877 in Eastern

¹ Cf. P. Knuth, 'Blumen und Insekten auf den nordfriesischen Inseln,' preface.

² Cf. P. Knuth, 'Die Besucher derselben Pflanzenart in verschiedenen Gegenden,' Part 2, conclusion.

Schleswig-Holstein (including the one self-contained territory, the Principality of Lübeck), and in Mecklenburg, besides isolated observations in Pomerania, Westphalia, Nassau, and Switzerland.

Willis and Burkill in Great Britain have gained credit by investigations on the floral oecology of fairly small districts (south and east coasts of Scotland, neighbourhood of Cambridge, and Mid-Wales); Scott-Elliot has done the same in Dumfries-shire, and Gibson in St. Kilda, which is very nearly the most remote island off the west coast of Scotland.

The floral arrangements of Arctic plants have been studied by Warming (Dovre-fjeld, Greenland), Lindman (Dovre-fjeld), Aurivillius, Holm and Ekstam (Nova Zemlia).

In North America Charles Robertson studies with untiring zeal the relations between flowers and insects in the neighbourhood of his home at Carlinville (Ill.).

Alfred R. Wallace has investigated the oecological relations between flowers and insects in a number of Pacific Islands (Fiji Is., Hayti, Juan Fernandez, New Zealand, Galapagos Is.). George M. Thompson has for several years worked very thoroughly the flower pollination of New Zealand, where he has also observed the pollination of flowers by birds. Thomas Belt noted this in Nicaragua, Fritz Müller in South Brazil, Hollingsworth in North America, Forbes in Sumatra, Scott-Elliot in South Africa, and Ferdinand v. Müller in Australia. The pollination of flowers by bats was observed by Burck in Java.

From among the numerous investigators who have been active in this field, of late years or quite recently, I may mention here, in addition to those already referred to, the following:—

1. Alps of Mid-Europe: v. Dalla Torre, Hoffer, and Kerner (Tyrol); A. Schulz (neighbourhood of Bozen); MacLeod (Maritime Alps); Calloni, Chodat, Christ, Frey, Frey-Gessner, Kirchner, Loew, Schröter (Switzerland); Hoffer (Steiermark).
2. Austria-Hungary (excluding 1): Bórbas, Burgerstein, Freyn, Gelmi, Hackel, Hansgirt, Kerner, Kronfeld, Rathay, Schilberszky, Velenovský, v. Wettstein, Wiesner, Willkomm.
3. South and Mid-Germany: Correns, Haussknecht, Kraus, Loew, Ludwig, Schenck, A. Schulz, Thomas.
4. North Germany: Alfken, Ascherson, Buchenau, Engler, Focke, Köhne, Loew, Magnus, Potonié, Ule, Urban, Warnstorf.
5. Denmark: Kjærskou, Lund, Raunkjær, Warming.
6. Scandinavia: Almqvist, Forsberg, Lagerheim, Lindman, Ljungström, Wittrock.
7. Russia: Batalin, Beketow, Borodin, Maximowicz.
8. Holland and Belgium: Giltay, Heinsius, de Vries, Vuyck.
9. British Isles: Archer-Briggs, Belt, A. W. Bennett, G. Bentham, Boulger, J. Britten, Burton, Christy, Cockerell, Comber, Dickie, Douglas, Duncan, Dyer, Evans, Farrer, Forbes, Fulton, Green, Hart, Henslow, J. D. Hooker, Keeble, Kitchener, John Lubbock, Marshall, Moggridge, S. Moore, Myers, Ogle, Powell, Ridley, W. S. Smith, Wetterhan, C. F. White, Whitelegge, Williams, Wilson, and others.

10. France: Baillon, G. Bonnier, Clavaud, Crié, Duval-Jouve, Giard, Godron, Guignard, Magnin, Maury, Roze.
11. Switzerland: Dodel-Port.
12. Italy: Arcangeli, Baroni, Beccari, Bonis, Buscalioni, Cobelli, Comes, Gibelli, Macchiati, Martelli, Mattei, Mori, Nicotra, Ottavi, Pasquale, Pedicino, Pirota, Ricasoli, Ricca, Savastano.
13. North America: Bailey, Barnes, Beach, W. J. Beal, Bessey, Bush, Courtis, Ellacombe, G. Engelmann, Foerste, Gentry, Greene, Halsted, Leggett, Martindale, Meehan, Pammel, Patton, Potts, Pringle, Redfield, C. V. Riley, Rusby, J. C. Russell, Schneck, C. J. Sprague, Todd, F. Ward, Webber, C. Wright, and others.
14. Tropical Regions: Balfour, Barber, Boissier, Evans, Faivre, Fitzgerald, Forbes, Gibbons, Greenleaf, Hartog, Haviland, Heckel, Hieronymus, Hunt, Irwin, Kellermann, Lynch, Moore, Murray, Nicholson, Parish, Rusby, W. G. Smith, Syme, Troop, E. Ule, F. Ward, Mansel Weale, Wright, and others.

Before I close this short survey of the historical development of flower pollination, I should like to mention a few other works in which the results of investigations on flower pollination are brought together.

That magnificent compilation, '*Die natürlichen Pflanzenfamilien*' (the early volumes of which were produced by Engler and Prantl together, but since the death of the latter (1893) has been edited by Engler alone), uniformly gives information as to the most important arrangements for pollination, in addition to the characters of the families.

The second volume of Anton Kerner von Marilaun's '*Natural History of Plants*' (Eng. Ed. 1, London and Glasgow, 1895) is an instance of the combination of scientific with popular presentation. The most important results of flower pollination are treated in the following chapters:—Protection of Pollen; Dispersion of Pollen by the Wind and by Animals; Allurements of Animals; The Colours of Flowers as a means of attracting Animals; The opening of the Passage to the Interior of the Flower; Reception of Flower-seeking Animals at the Entrance to the Flower; Taking up of Pollen by Insects; Deposition of Pollen; Crossing of Flowers; and Autogamy. The comprehension of the subject is made easy even for the lay mind by excellent illustrations. As a result of the above division, it is, however, necessarily troublesome to get information on all the floral arrangements of particular plants.

The '*Lehrbuch der Biologie der Pflanzen*' by F. Ludwig (Stuttgart, 1895) brings together in its fourth division what is most important in flower pollination: Hydrophily, Anemophily, Zoidiophily, as well as examples of floral adaptations to the agents that effect fertilization.

The work already mentioned, '*Blütenbiologische Floristik des mittleren und nördlichen Europas sowie Grönlands*,' by E. Loew (Stuttgart, 1894), as stated in the preface, summarizes in the briefest possible way all the researches in flower pollination published between 1884 and 1894. It forms a supplement to the pioneer works of Hermann Müller, '*Die Befruchtung der Blumen durch Insekten*' and '*Alpenblumen*,' and therefore the descriptions of arrangements for pollination contained in Müller's books are not repeated, but are completed by newer

observations. On the other hand, processes of pollination that were not described by Müller, and plants investigated by later observers, are treated at somewhat greater length. Occasionally, Loew goes back to older publications when this seems necessary for the completion of his accounts. Owing to the exigencies of space, lists of visitors had to be excluded, but in the case of certain plants at least the chief groups of the flower visitors are given, together with an enumeration of species. Loew's 'Blütenbiologische Floristik' has been an indispensable work of reference for me during the production of this work, and many facts have been taken from it.

SECOND SECTION

PRESENT STANDPOINT OF FLOWER POLLINATION

I. Survey of the Modes of Pollination and of the Distribution of the Sexes.

The following chief kinds of pollination and fertilization are known to us at the present time :—

(I) **Autogamy** (Delpino), or Self-pollination: the pollen reaches the stigma of the same flower. Autogamy is therefore only possible in hermaphrodite flowers. When effective the result is Autocarp, or Self-fertility; if not effective, Self-sterility.

(a) *Direct Autogamy* (Spontaneous Self-pollination) depends upon the relative positions of stigma and anthers, without reference to external agency. If it is effective the result is Direct Autocarp.

(b) *Indirect Autogamy* (Self-pollination in the narrower sense) is brought about by external agency. If effective the result is Indirect Autocarp.

(II) **Allogamy** (Kerner), or Cross-pollination. The pollen reaches the stigma of another flower. If effective the result is Allocarp; if non-effective there is Adynamandry.

(a) *Geitonogamy* (Kerner), or Pollination by a neighbour, occurs between flowers of the same plant. If it is effective the result is Geitonocarp.

(b) *Xenogamy* (Kerner), or Crossing, occurs between flowers of different plants of the same species. If effective the result is Xenocarp.

(III) **Hybridization** occurs between flowers of different species. If effective the result is Hybridocarp.

The most important known ways in which the sexes are distributed, as well as the various possibilities of pollination conditioned by the arrangement of stamens and carpels, may be summarized as follows¹:—

¹ Cf. Kirchner, 'Flora von Stuttgart' (pp. 38-40).

A. ALL FLOWERS ARE UNISEXUAL: Dicliny (Division of sexes). Only Allogamy possible.

1. Male and female flowers on the same plant: Monoecism (Linnaeus) or One-house plan. Geitonogamy and Xenogamy are possible.

2. Male and female flowers on different plants: Dioecism (Linnaeus) or Two-house plan. Only Xenogamy is possible.

B. ALL FLOWERS ARE HERMAPHRODITE: Monocliny (Linnaeus) or Bi-sexuality.

1. The stigmas and anthers of the same flower are not simultaneously mature: Dichogamy (Sprengel). If this peculiarity is so well marked that the stigmas have dried when the anthers spring up, or vice versa, only Cross-pollination is possible. If it is not so well marked, Self-pollination is possible later on. Dichogamy appears in two forms:—

(a) The anthers are ripe before the stigmas have developed: *proterandry* (Delpino) or *protandry* (Hildebrand).

(b) The stigmas are ready to receive pollen before the anthers dehisce: *proterogyny* (Delpino)¹, *protogyny* (Hildebrand).

2. The stigmas and anthers of a flower are simultaneously mature: Homogamy (Sprengel).

a. The flowers are open at the time of the maturity of stigma and anthers: **Chasmogamy** (Axell).

a. Spontaneous self-pollination is impossible in consequence of the relative positions of stigma and anthers: *Herkogamy* (Axell).

β. Spontaneous self-pollination is rendered possible by the relative positions of stigma and anthers:

(α) All flowers are similarly constructed as regards length of style and stamens: *Homomorphy* or *Homostyly* (Hildebrand).

(β) On different plants there are flowers distinguished by a difference in length of stamens and style: *Heteromorphy*.

* The styles and also the stamens are of different lengths: *Heterostyly* (Hildebrand).

† Two different forms of flowers occur: some with long styles and short stamens, others with short styles and long stamens: *Dimorphism* (or better, *Heterodistyly*).

†† Three different forms of flowers occur: some with long styles and medium and short stamens, others with medium styles and long and short stamens, others with short styles and long and medium stamens: *Trimorphism* (or better, *Heterotristyly*).

** Only the stamens are of different lengths: *Heteranthery*.

β. The flowers are closed at the time of maturity of stigma and anthers: **Cleistogamy** (Kuhn).

¹ Delpino distinguishes (1) *Proterogynia brachybiostigmata*, that is *Proterogyny* with short-lived stigmas, if the stigmas fade before the anthers burst so that self-pollination is prevented, and (2) *Pr. macrobiostigmata* (Pr. with persistent stigmas) when the stigmas remain capable of receiving pollen till the anthers are ripe, so that self-pollination is at least possible.

- a. The flowers all remain permanently closed: *archo-cleistogamy* (Knuth).
- β. Besides cleistogamous flowers there occur others that are chasmogamous: *chasmo-cleistogamy* (Delpino).
- γ. The flowers remain closed only under certain circumstances: *pseudo-cleistogamy* (Hansgirg). This may occur.
 - (a) In consequence of deficiency of light: *photo-cleistogamy*.
 - (β) In consequence of a high water-level: *hydro-cleistogamy*.
 - (γ) In consequence of insufficient warmth: *thermo-cleistogamy*.
- δ. The flowers open a little: *hemi-cleistogamy* (Knuth).
 - (a) The stamens project: *chasmanthery*¹.
 - (β) The stamens remain enclosed: *cleistanthery*¹.

C. IN THE SAME SPECIES MONOCLINOUS AND DICLINOUS FLOWERS OCCUR: Polygamy (Linnaeus).

- 1. All the floral forms occur on the same plant.
 - a. Hermaphrodite and male flowers occur: **Andro-monoecism** (Darwin).
 - b. Hermaphrodite and female flowers occur: **Gyno-monoecism** (Darwin).
 - c. Hermaphrodite, male, and female flowers occur: **Coeno-monoecism** (Kirchner).
- 2. Monoclinous and diclinous flowers appear on different plants.
 - a. Hermaphrodite and male plants occur: **Androdioecism** (Darwin).
 - b. Hermaphrodite and female plants occur: **Gynodioecism** (Darwin).
 - c. Hermaphrodite, male, and female plants occur: **Trioecism** or **trioecious polygamy** (Darwin).

By the researches of F. Ludwig, O. Kirchner, A. Schulz, and E. Warming, besides the already mentioned modes of distribution of the sexes numerous others have been made known. In particular, it appears from the observations of these investigators that many plants may be simultaneously andromonoecious and androdioecious, or gynomonoecious and gynodioecious, or at the same time andromonoecious, androdioecious, gynomonoecious, and gynodioecious. For such cases Loew (Humboldt, viii, pp. 197 et seq.) has proposed the term **Pleogamy**.

We are especially indebted for important researches on this subject to Aug. Schulz, who has published them in his 'Beitrag zur Kenntnis der Bestäubungs-einrichtungen und Geschlechtsverteilung bei den Pflanzen,' I and II (Bibliotheca botanica, Nos. 10 and 17). The most important of the instances recorded by Schulz are summarized by Loew ('Blütenbiol. Floristik,' pp. 377-81) as follows:—

Group 1.—In many stocks that are fundamentally hermaphrodite, the stamens of all the hermaphrodite flowers degenerate; on others, this is the case only in certain flowers. The individuals are therefore of three kinds: Hermaphrodite, female,

¹ The terms cleistanthery and chasmanthery, having already been used in another sense, must retain this by right of priority. Ascherson (Ber. D. bot. Ges., x, 1892) applies the term chasmantherous to those cleistogamous flowers in which the anthers dehisce, shedding their pollen-grains on to the stigma, where they germinate (e.g. in *Vicia angustifolia*); the term cleistantherous, on the other hand, is applied to those cleistogamous flowers in which the anthers do not dehisce, so that the pollen-tubes are obliged to penetrate the anther walls before they can reach the stigma.

[Knuth does not devise fresh terms to replace those superseded. Cryptantherous and crypt-anthery, phaenanthery and phaenanthery, are here suggested.—Tr.]

and hermaphrodite-female, that is, gynodioecism is united with gynomonoeicism : **Female Pleogamy.**

To this group belong :—Hepatica, species of Ranunculus, most of the German species of Dianthus, many Lychnideae, almost all Alsineae, many species of Geranium, Potentilla, Epilobium, also Ribes Grossularia, Saxifraga oppositifolia, Sherardia arvensis, most Dipsacaceae, Convolvulus, Anchusa, Echium, species of Verbascum and Digitalis, most German Labiatae, species of Plantago, Polygonum amphibium, and others.

Group 2.—In many stocks that are fundamentally hermaphrodite some of the carpels degenerate, in others they all degenerate. The individuals are therefore again of three kinds : Hermaphrodite, male, and hermaphrodite-male, i.e. androdioecism is united with andromonoeicism : **Male Pleogamy.**

To this group belong :—Pulsatilla alpina, Dryas octopetala ; Geum urbanum, rivale, reptans, and montanum ; many species of Rubus, Asperula taurina, Chenopodium glaucum and vulvaria, Veratrum album.

Group 3.—In many stocks that are fundamentally hermaphrodite, the stamens degenerate in all or some flowers. Similarly, in other hermaphrodite stocks the carpels degenerate in all or some of the flowers. In yet other stocks degeneration does not usually occur, though it occasionally affects the stamens and carpels of different flowers on the same plant. We have here, therefore, andromonoeicism, androdioecism united with gynomonoeicism, and gynodioecism, so that five different series of individuals commonly result, while to these may sometimes be added a supplementary series of trimonoeicious individuals. By the increasing suppression of hermaphrodite flowers and hermaphrodite plants, there appears in this group a tendency towards the formation of purely dioecious plants, but three stages may still be distinguished :

1. *The hermaphrodite forms predominate markedly, while the pleogamous forms are very common.*

Euonymus europaeus. Mostly hermaphrodite. Among several thousand shrubs will be found only 1–3 purely unisexual individuals. Gynomonoeicism and andromonoeicism are here and there more common.

Fragaria vesca. Mostly hermaphrodite. The pleogamous forms are sometimes entirely wanting. They occur in approximately equal numbers.

F. collina. Purely hermaphrodite forms nearly always predominate. Pleogamous forms are always rather more abundant than in the preceding species.

Plantago media. Mostly hermaphrodite. Female-pleogamous forms, when present, amount to 2–3 %. Male-pleogamous forms are still scarcer.

Swertia perennis. Occasionally gynomonoeicious, rarely gynodioecious, andromonoeicious, or androdioecious.

2. *Hermaphrodite forms less dominant, while pleogamous forms appear somewhat more frequently. Among the latter either female or male may predominate, or they may occur in approximately equal numbers.*

(a) FEMALE FORMS PREDOMINATE.

Geranium sylvaticum. Female-pleogamous up to 25 %. Male forms scarce,

sometimes apparently absent (Thuringia and Riesengebirge) or occurring sporadically (Tyrol): perhaps more abundant in North Europe.

Erodium cicutarium. Female-pleogamous 5-30%; male forms scarce and isolated.

Valeriana montana. Mostly gynodioecious, frequently also gynomonoecious. Isolated ♂ plants, or, rarely, ♂ and ♀ on the same plant.

Polygonum viviparum. Female-pleogamous up to 30%; male-pleogamous usually only 1-2%, never more than 10%.

P. Fagopyrum. Gynomonoecious up to 20%; sporadically gynodioecious, andromonoecious, or androdioecious.

Thymus Chamaedrys. Gynodioecious up to 40-50%, or even more; very seldom gynomonoecious; observed by Ogle in England and Delpino in Italy to be also androdioecious.

Viscaria vulgaris. Usually gynodioecious, seldom gynomonoecious; ♀ in some localities up to 20%. Male pleogamous forms, when present, only 2-5%.

Coronaria Flos cuculi. Gynodioecious, seldom gynomonoecious up to 10% at most. Male-pleogamous forms at most 3%.

Silene rupestris. Gynodioecious and gynomonoecious up to 5%. Male-pleogamous forms very scarce.

S. nutans. Female forms up to 10%; male (if present) up to 5%.

Saponaria ocymoides. Gynodioecious or gynomonoecious forms up to 5%. Male-pleogamous forms very scarce.

(b) MALE FORMS PREDOMINATE.

Daucus Carota. Andromonoecious, frequently also gynodioecious, seldom gynomonoecious.

Pimpinella Saxifraga. Andromonoecious, less frequently gynodioecious.

Scleranthus annuus. Male-pleogamous widely distributed, usually 5-10%; female scarce and isolated.

Pulsatilla vulgaris, *montana*, *pratensis*, and *vernalis*. Occasionally andromonoecious and androdioecious, now and then also gynomonoecious and gynodioecious.

(c) FEMALE AND MALE FORMS ABOUT EQUALLY COMMON.

Scleranthus perennis. Female-pleogamous forms widely distributed, often 30% or more; male, if present, numerous.

Silene vulgaris. Gynodioecious; less frequently gynomonoecious, sometimes only 1-2%, sometimes 50% or more. In plains, fairly often androdioecious; with wide distribution; less frequently andromonoecious, ♂ often up to 20%. In mountains, ♂ forms are often wanting.

S. noctiflora. Gynodioecious, forms widely distributed, gynomonoecious less frequently. ♂ forms unequally distributed, rare in places.

Valeriana tripteris. In South Tyrol usually gynodioecious and gynomonoecious; locally andromonoecious and androdioecious, sometimes even ♀ and ♂, or ♀, ♀, and ♂ on the same plant.

Poterium Sanguisorba. Usually ♂, ♀, and ♀ on the same plant, occasionally also gynomonoecious, or andromonoecious, or purely monoecious.

Rumex maritimus and other species. Frequently gynomonoecious, less frequently gynodioecious. Sometimes purely ♂ and ♀ stocks.

Alchemilla vulgaris, *fissa*, *alpina*, and *pentapetala*. Male- and female-pleogamous forms locally replace hermaphrodites.

3. *Dioecism predominates; the sexes about equally well represented. Hermaphrodite and pleogamous forms are not numerous.*

Silene Otites and *acaulis*. Almost exclusively dioecious.

Melandryum album. Dioecious. ♂ and ♀ equally common. Hermaphrodite forms very rare.

M. rubrum. Usually dioecious. ♂ and ♀ sometimes equally common, sometimes one (generally ♀) predominating. Hermaphrodite plants commoner than in the preceding species (often up to 5%). Sporadically monoecious, very rarely andromonoecious.

Fragaria elatior. In some places dioecious, in other places purely hermaphrodite flowers (up to 10%); in places only female- and male-pleogamous, often gynomonoecious; on the other hand, andromonoecious individuals are occasionally altogether absent.

Rubus Chamaemorus. Dioecious. In the Riesengebirge sometimes almost completely falsely hermaphrodite.

Valeriana dioica. Usually dioecious, ♀ usually in two forms; ♀ rare and local.

V. saxatilis. ♂ and ♀ plants equally common, ♀ sporadic; may also be andromonoecious and gynomonoecious, frequently ♀ and ♂, rarely ♀, ♂, and ♀ on the same plant.

Trinia glauca. ♂ and ♀ plants about equally common. Various pleogamous forms occur locally.

Rumex Acetosa, *Acetosella* and *arifolius*. ♂ and ♀ plants equally common, rarely gynomonoecious, or andromonoecious, or hermaphrodite.

Rhodiola rosea. Dioecious (in the Riesengebirge according to Schulz, on the Dovrefjeld according to Lindman) or trioecious (in the Alps according to Ricca, in Greenland according to Warming).

Empetrum nigrum. In the North Frisian Islands trioecious, with very rare hermaphrodite forms (Buchenau), similarly on the Dovrefjeld (Lindman); in Greenland only dioecious (Warming).

Asparagus officinalis. Usually dioecious; rarely purely hermaphrodite, andromonoecious, and gynomonoecious plants.

The above-mentioned investigations, undertaken by Schulz with great care and perseverance, still require much amplification to make them complete. On this point Loew ('Blütenbiol. Floristik,' p. 392) remarks that 'Progress in this sphere is only possible by correlated and systematized work, conducted by many investigators.'

II. Autogamy.

Kerner ('Nat. Hist. Pl.,' Eng. Ed. I, II, pp. 331-401) has treated at length the various kinds of Autogamy, and especially distinguishes between the following categories:—

1. The anthers lie close to the stigmas, covering these when they open. This occurs more especially in small annual plants, such as *Centunculus minimus*, species of *Drosera*, *Lepidium ruderae*, *Geranium pusillum*, *Lithospermum arvense*, and others, and also in a number of Liliaceae, as e. g. some species of *Fritillaria*, *Narcissus*, *Trillium*, *Uvularia*, *Crocus*.

2. In pendulous flowers with anthers united into a cone, the filaments relax when the flower is nearly mature, so that the loculi are no longer so closely apposed, and the mealy pollen falls on the underlying stigmas; e. g. *Galanthus*, *Soldanella*, *Dodecatheon*.

3. In erect flowers, when the walls of the anthers contract, pollen falls on the stigma, which lies vertically beneath: *Narthecium*, *Tofieldia*.

4. In erect funnel-shaped flowers, the pollen glides along the smooth inner wall of the corolla to the deeply seated stigma: *Syringa*.

5. During flowering the filaments elongate, so that the anthers, which are to begin with at a lower level than the stigma, finally reach the same level, and pollinate it: *Adoxa Moschatellina*, species of *Scleranthus*, *Paederota Bonarota*, many Cruciferae, species of *Saxifraga*, small-flowered species of *Epilobium* and *Geranium*, *Ipomaea purpurea*, *Agrostemma Githago*, *Saponaria Vaccaria*, *Silene conica*.

6. The straight filaments are at first directed outwards, keeping the anthers away from the stigma, so that self-pollination is not possible; later on the stamens incline towards the middle of the flower, so that the pollen-covered anther-lobes touch the stigma, and pollinate it: *Azalea procumbens*, *Draba aizoides*, numerous Saxifragaceae, Alsineae, Cruciferae, *Hypericum perforatum*, *Oxalis stricta*, *Ornithogalum umbellatum*, *Paris quadrifolia*, species of *Scilla*, *Chelidonium*, *Samolus Valerandi*, species of Androsace, *Lysimachia nemorum*, *Swertia perennis* and *punctata*.

7. The filaments are from the first inwardly curved; later on they incline still further inwards, till they either come in contact with the stigma, or are perpendicularly above and able to shower down pollen upon it: numerous Compositae, species of *Galium* and *Cuscuta*, *Circaea alpina*, *Agrimonia Eupatoria*, small-flowered species of *Sedum*, *Opuntia*, species of *Rosa*, *Hepatica triloba*; species of *Ranunculus*, *Gypsophila*, and *Saxifraga*; *Cuphea*, *Nicandra*.

8. The style at first projects beyond the anthers, but shortens later on, so that ultimately the anthers (still covered with pollen) come into contact with the stigma: species of *Cereus*, *Echinopsis*, and *Mammillaria*.

9. Autogamy results from the lengthening of the ovary or of the style: *Epimedium alpinum*, *Sinapis arvensis*, *Atragene alpina*, *Clematis integrifolia*, *Alchemilla vulgaris*.

10. Autogamy results from inclination of the style, which, however, remains straight: *Collinsonia canadensis*.

11. Autogamy results from bending of the style, so that the stigma is either brought into immediate contact with the pollen-covered anthers, or assumes such

a position that pollen can fall upon it: *Verbascum Thapsus*, species of *Valerianella*, the non-twining species of *Lonicera*, *Lilium Martagon*, species of *Oenothera* and *Epilobium*, *Tricyrtes*, *Morina*; various *Scrophulariaceae*, *Caryophyllaceae*, and *Ranunculaceae*; most *Malvaceae*.

12. By curvature of the stigma: species of *Galeopsis* and *Stachys*, *Pinguicula*, *Utricularia*.

13. Towards the end of the period of maturity the filaments and the style roll together in a spiral or screw-like way, getting tangled together, so that pollen and stigma come into contact: *Commelina coelestis*, *Allionia violacea*, *Mirabilis Jalapa*, *Portulaca oleracea*, *Armeria vulgaris* and *alpina*.

14. Autogamy by shrinking, or spiral rolling back, of the branches of the stigma: numerous *Campanulaceae* and still more numerous *Juncaceae*, *Dianthus glacialis* and *neglectus*, *Ballota nigra*.

15. Autogamy by the agency of petals in one of the following ways:— (1) anthers united to the inner side of the corolla, and the stigma comes into contact with and receives pollen from them on the closing of the flower (*Thymelaea passerina*); (2) anthers united with the inner side of the corolla, to begin with at a lower level than the stigma, but ultimately reaching the same level by the growth of the corolla (many *Solanaceae* and *Gentianaceae*; some species of *Euphrasia* and *Rhinanthus*); (3) the stigma is drawn through the falling corolla, so that it touches the anthers still laden with pollen, or receives pollen that has adhered to the inner side of the corolla (*Rhododendron hirsutum*; *Digitalis*, *Anchusa*, *Cestrum*, and other *Scrophulariaceae*, *Boraginaceae*, and *Solanaceae*); (4) towards the end of the period of maturity the petals execute movements, so that the pollen adhering to their margins, surfaces, lobes, or folds, reaches the stigma either (a) without elongation of the petals (*Argemone*, *Hypecoum*, *Specularia*), or (b) with elongation of the petals (*Gentiana asclepiadea*, *G. Pneumonanthe*, *Colchicum*, *Sternbergia*, *Sisyrinchium*, *Crepis*, *Hieracium*, *Hypochaeris*, *Leontodon*); (5) by actual bending of the corolla at the end of the period of maturity, when either mealy pollen falls on the stigma (*Pedicularis incarnata*, *Oederi*, *foliosa*, *comosa*, and *recutita*; *Melampyrum sylvaticum*), or else the anthers, covered with sticky pollen, come into contact with the stigma (the climbing species of honeysuckle—*Lonicera Caprifolium*, *etrusca*, and *Periclymenum*).

16. Towards the end of the period of maturity the pollen reaches the stigma as the result of changes in the position and direction of the flower-stalk, while the position and direction of the stamens, style, and stigma remain unchanged: *Tulipa sylvestris*, *Polemonium coeruleum*, *Saxifraga hieracifolia*, *Chrysosplenium alternifolium*, *Rhododendron Chamaecistus*, *Vaccinium*, *Arctostaphylos*, *Cerinth*, *Symphytum*, *Cyclamen*, *Calceolaria Pavonii*.

17. Autogamy by correlated movements and curvings of flower-stalk, stamens, and style:—*Ornithogalum nutans*, *Dryas octopetala*; *Geum coccineum*, *montanum*, and *reptans*; *Potentilla atrosanguinea* and *repens*; *Waldsteinia geoides*, *Adonis vernalis*; *Anemone alpina* and *baldensis*; *Pyrola uniflora*, *Phygellus capensis*, *Cobaea scandens*, *Allium Chamaemoly*.

18. Autogamy by correlated curving of the flower-stalk, and curving or folding of the petals: species of *Viola*; *Gentiana acaulis*, *angustifolia*, and *Clusii*.

19. Autogamy by correlated curving of the flower-stalk, and elongation of the petals: *Pulsatilla vulgaris* and *vernalis*.

20. Autogamy by correlated curving of the flower-stalk, lengthening of the petals, lengthening of the stamens, and curving of the style: *Geum rivale*; *Rubus Idaeus* and some related forms.

The effect of the pollen on the stigma of the same flower is very varied. There are numerous cases known in which it is absolutely inactive (*self-sterility*), but in still more numerous instances there is no considerable difference between the effect of pollen of the same plant, and foreign pollen (*self-fertility*). If pollen from the same plant and pollen from another plant get to the stigma, it has been proved in many cases that the latter is more effective than the former—i.e. the foreign pollen predominates or is *prepotent*.

The investigations of different observers with regard to the self-sterility and self-fertility of many plants have not infrequently given contradictory results. Thus, for example, according to Hildebrand and Kirchner, rape (*Brassica Rapa*) is self-fertile, while, according to Lund, Kjærskou, and Focke, it is self-sterile, so that we must assume that self-sterility is a character that is not constant for all individuals of the same species, but varies with the locality and the individual.

The best-known cases of **Self-sterility** or infertility of a plant as regards its own pollen are as follows:—

Ranunculaceae.—*Ranunculus acris* (Focke), perhaps also *R. bulbosus* (Focke). *Nigella damascena* (Hoffmann). *Delphinium Consolida* (Darwin).

Papaveraceae.—Cultivated specimens of *Papaver alpinum* (H. Hoffmann), *P. Rhoeas* (Hoffmann), *P. somniferum* (Hoffmann), *P. nudicaule* (Focke). *Eschscholtzia californica* (Fr. Müller, Chas. Darwin). *Hypocoum grandiflorum* (Hildebrand).

Fumariaceae.—*Dielytra spectabilis* (Delpino). *Corydalis cava* and *solida* (Hildebrand).

Cruciferae.—*Brassica Rapa* (Focke, Lund, and Kjærskou). *Raphanistrum arvense* (Hoffmann). *Dentaria bulbifera* (Delpino, Knuth).

Cistaceae.—Hybrid forms of *Cistus* (Bornet).

Violaceae.—Large-flowered specimens of *Viola tricolor* (Hermann Müller), *V. canina* (Darwin).

Silenaceae.—*Dianthus Caryophyllus* (Darwin).

Resedaceae.—Some specimens of *Reseda odorata* (Darwin), and of *R. lutea* (Darwin, Focke).

Malvaceae.—*Abutilon Darwinii* Hook. (Fritz Müller, Darwin), *A. striatum* Dicks., *A. venosum* Hook., *A. forma hybr.* (Fr. Müller).

Geraniaceae.—*Erodium macradenum* (Fr. Ludwig). *Pelargonium zonale* (Darwin).

Onagraceae.—Sp. of *Fuchsia* (Gärtner).

Lythraceae.—*Cuphea purpurea* (Gärtner).

Melastomaceae.—*Centradenia floribunda*, *Rhexia glandulosa*, *Pleroma*, *Monochaetum ensiferum*, *Heterocentron mexicanum* (Darwin).

Rosaceae.—*Rubus odoratus* and *spectabilis* (Focke). *Kerria japonica* and *Neviusia alabamensis* in Europe (Focke).

Pomaceae.—*Pyrus communis* (Swayne, Waite, Focke). *Cydonia japonica* (Focke).

Amygdalaceae.—*Prunus* (*Chamaecerasus*) *incana* Stev. (Focke), *P. lusitanica* (Focke).

Papilionaceae.—*Trifolium pratense*, *repens*, and *incarnatum*; *Phaseolus multiflorus*, *Lathyrus grandiflorus* (in England), *Vicia Faba*, sp. of *Erythrina*, *Sarothamnus scoparius*, *Melilotus officinalis*, *Lotus corniculatus*, *Cytisus Laburnum* (Darwin). *Astragalus alpinus* (Axell). *Wistaria sinensis* (Gentry).

Calycanthaceae.—*Calycanthus floridus* (Meehan).

Passifloraceae.—*Passiflora alata*, *racemosa*, *laurifolia* (rare observations on greenhouse plants), *quadrangularis* (Mowbray, Scott), and other species.

Cactaceae.—*Cereus grandiflorus* Miller (Neubert and others).

Compositae.—*Senecio cruentus* (Darwin).

Goodeniaceae.—*Leschenaultia tubiflora* (Darwin).

Campanulaceae.—*Campanula carpathica* (Darwin).

Lobeliaceae.—A few individuals of *Lobelia fulgens* (Gärtner), *L. cardinalis* (Focke), *L. ramosa* (Darwin). Species of *Isotoma* (Darwin).

Ericaceae.—*Kalmia latifolia* (Beal).

Jasminaceae.—*Jasminum grandiflorum* and *officinale* (Delpino).

Oleaceae.—*Forsythia viridissima* (Delpino), *Calonyction Choisy*. (Darwin).

Gentianaceae.—*Lysimachia nummularia* L. (Darwin, Warming).

Solanaceae.—*Lycium rhombifolium* (Focke). *Petunia violacea* (Darwin). Some varieties of *Solanum tuberosum* (Tinzmann).

Labiatae.—*Salvia Tenori* and *coccinea* (Darwin).

Scrophulariaceae.—*Linaria vulgaris*, varieties of *Antirrhinum majus*, *Digitalis purpurea* (Darwin). One individual of *Verbascum nigrum* (Gärtner), several individuals of *V. phoeniceum* (Kölreuter, Gärtner, Focke), *V. phlomoides* (Focke).

Primulaceae.—*Primula scotica* and *Cortusa Matthioli* (Scott). *Cyclamen persicum* (Darwin).

Boraginaceae.—*Borago officinalis* (Darwin).

Apocynaceae.—*Apocynum androsaemifolium* (Ludwig). *Tabernaemontana echinata* Aubl. (Fr. Müller). *Vinca major* and *rosea* (Darwin).

Asclepiadaceae.—*Stephanotis floribunda* Brug. (Delpino). *Hoya carnosa* R. Br. (Delpino). *Periploca graeca* L. (Delpino).

Bignoniaceae.—Species of *Bignonia* (Fr. Müller). *Tecoma grandiflora* Delaun. (Delpino).

Daphnaceae.—A cultivated specimen of *Daphne Mezereum* in Thuringia (Fr. Ludwig).

Cupuliferae.—*Castanea americana* (Schneck).

Scilaminaceae.—*Hedychium coccineum* (Fr. Müller). *Alpinia nutans* Rosc. (Fr. Müller), a sp. of *Alpinia* (Fr. Müller). *Zingiber officinale*, probably (Focke).

Orchidaceae.—Numerous indigenous and exotic species (Darwin¹). *Maxillaria atrorubens* and others (Scott). *Epidendrum cinnabarinum* (Fr. Müller). *Oncidium phacelatum* (Scott, Munro), *O. Lemonianum* (Eggers), *O. divaricatum* (Munro), *O. microchilum* (Scott), *O. Cavendishianum* (Rivière), *O. flexuosum* (Fr. Müller),

¹ Self-fertilization is a rare phenomenon among Orchids (Darwin, 'Orchids').

O. crispum, some examples, and other sp. of *O.* (Fr. Müller). Sp. of *Notylia*, *Burlingtonia*, *Rodriguezia*, *Gomezia*, and (?) *Stigmatostalix* (Fr. Müller).

Bromeliaceae.—*Billbergia speciosa Riv.* (Fr. Müller).

Araceae.—*Atherurus ternatus* (Hunger).

Liliaceae.—*Lilium candidum* (Tinzmann), *L. croceum Chaix* (Focke), *L. bulbiferum* (Focke, Neubert), *L. canadense* (Meehan). *Hemerocallis flava*, *Dumortieri*, and *serotina* (Focke), *H. fulva* (Sprengel, Maximowicz, Hoffmann).

Amoryllidaceae.—*Pancratium caribaeum* (Eggers). *Hippeastrum aulicum* (Herbert), hybrid forms of *Hippeastrum* (Herbert).

Iridaceae.—*Romulea Bulbocodium* var. *dioica Seb. et Maur.* (Battandier). Hybrid forms of *Gladiolus* (Rawson). *Marica Northiana* (Fr. Müller).

Gramineae.—*Secale cereale* (Rimpau, Liebenberg, Focke, Beijerinck). *Saccharum officinarum L.*, probably (Focke).

Self-sterility is often associated with unusual powers of vegetative propagation. In many cases related species behave differently with respect to their fertility or infertility as regards their own pollen. For example:—

Self-sterile.

Ranunculus acris (Focke).

R. bulbosus? (Focke).

To these may be added the following Brazilian instances given by Fritz Müller (Abh. natw. Ver., Bremen, xii, 1893, p. 495):—

Abutilon striatum Dicks.

A. venosum Hook.

A. Darwinii Hook. f.

A. form hybr.

Billbergia speciosa Riv.

Marica Northiana Ker.

Hedychium coccineum Sm.

Alpinia nutans Rosc.

A. sp.

Self-fertile.

R. auricomus (Focke).

R. arvensis (Focke).

A. megapotamicum A. St. Hil. et Naud.

Billbergia zebrina Lindl.

Marica sp. al.

Cypella sp.

Trimeriza sp.

H. coronarium Koem.

Alpinia sp.

The following are **Self-fertile**, i.e. perfectly fruitful (or, at least, not greatly weakened) in the absence of insects¹:—

Ranunculaceae.—*Ranunculus acris* (Darwin, but self-sterile according to Focke), *R. auricomus* (Focke), *R. arvensis* (Focke). *Adonis aestivalis* (Hoffmann).

Nymphaeaceae.—*Papaver somniferum* (Darwin), *P. dubium* (Hoffmann), *P. vagum* (Darwin), *P. argemonoides* (Hildebrand), *P. nudicaule L.* (Warming). *Glaucium luteum* (Hildebrand). *Argemone ochroleuca* (Darwin). *Adlumia cirrhosa* (Darwin). *Hypecoum procumbens* (Hildebrand).

Fumariaceae.—*Fumaria officinalis* (Darwin, Hoffmann), *F. capreolata* (Darwin). *Corydalis ochroleuca* (Kerner).

¹ In addition to the cases of self-fertility given here, many others have been described, especially by Henslow, Meehan, Pedicino, and Wilson. It is impossible to enumerate them in this place (cf. p. 23).

Cruciferae.—*Brassica fruticosa* *Cyr.* (Comes), *B. oleracea* (Darwin, Lund, and Kjærskou), *B. Napus* (Lund, Kjærskou). *Raphanus sativus* (Darwin). *Subularia aquatica* (Hiltner, Knuth). *Iberis umbellata* (Darwin), *I. amara* (Darwin). *Cochlearia danica* *L.* (Knuth). *Diploaxis erucoides* *DC.* (Comes). *Draba rupestris* *R.Br.* (Comes). *Myagrum perfoliatum* *L.* (Comes). *Bunias Erucago* *L.* (Comes). *Erysimum amoenum* *Breb.* (Comes). *Sisymbrium officinale* *L.* (Comes). *Lepidium ruderae* *L.* (Comes, Knuth). *Erophila*, short-fruited form (F. Rosen). *Capsella Bursa-pastoris* (Herm. Müller, Anna Bateson).

Resedaceae.—*Reseda odorata* and *lutea*, some individuals (Darwin).

Malvaceae.—*Althaea ficifolia* *Cav.* (Comes). *Abutilon megapotaemicum* (Fr. Müller).

Violaceae.—*Viola tricolor*, small-flowered (Herm. Müller).

Droseraceae.—*Drosera rotundifolia* and *intermedia* (Knuth).

Caryophyllaceae.—*Viscaria oculata* (Darwin). *Stellaria media* (Darwin, Herm. Müller, Anna Bateson, Warming). *Sagina nivalis* *Fr.*, *S. caespitosa* *I. Vahl*, *Alsine biflora* *Wahlbg.*, *A. stricta* *Wahlbg.* (Warming). *Cerastium tetrandrum* *Curtis* (Knuth). *Gypsophila elegans* *Bilb.* (Comes).

Linaceae.—*Linum usitatissimum* (Darwin, Hoffmann).

Hypericaceae.—*Hypericum hirsutum* *L.*, probably (Herm. Müller).

Geraniaceae.—*Erodium cicutarium* (Ludwig).

Limnanthaceae.—*Limnanthes Douglasii* (Darwin).

Balsaminaceae.—*Impatiens barbiger* (?) and *I. Noli-tangere* (Darwin), *I. parviflora* (Henslow, Knuth).

Papilionaceae.—*Vicia sativa*, *V. hirsuta*, *Pisum sativum*, *Lathyrus odoratus* *L.*, *Nissolia*, *Lupinus luteus*, *L. pilosus*, *Ononis minutissima*, *Phaseolus vulgaris*, *Trifolium arvense*, *T. procumbens*, *Medicago lupulina* (Darwin). *Ornithopus perpusillus* (Knuth).

Onagraceae.—*Epilobium alpinum* (Axell). *Godetia Lindleyana* *Spach.* (Comes).

Lythraceae.—*Cuphea silenoides* *Nees*, *C. floribunda* *Lehm.*, and *C. Melvilla Lindl.* (Treviranus).

Passifloraceae.—*Passiflora gracilis* (Darwin).

Umbelliferae.—*Helosciadium inundatum* (Knuth). *Apium petroselinum* (Darwin).

Paronychiaceae.—*Herniaria hirsuta* (Delpino).

Rubiaceae.—*Galium Aparine* (Darwin).

Saxifragaceae.—*Saxifraga nivalis* *L.*, *S. rivularis* *L.*, *S. decipiens* *Ehrh.*, *S. oppositifolia* *L.*, and *Chrysosplenium tetrandrum* *Th. Fr.* (Warming).

Dipsacaceae.—*Scabiosa ochroleuca* *L.* (Comes).

Compositae.—*Lactuca sativa* (Darwin). *Senecio vulgaris* (Herm. Müller, Anna Bateson). *Hieracium alpinum* (Hoffmann).

Campanulaceae.—*Specularia speculum* (Darwin).

Convolvulaceae.—*Convolvulus tricolor* *L.* (Comes). *Ipomoea purpurea* and *Nolana prostrata* (Darwin).

Polemoniaceae.—*Leptosiphon androsaceus* (Darwin). *Collomia linearis* *Nutt.* (Comes).

Vacciniaceae.—*Vaccinium Vitis-Idaea* *L.* var. *pumilum* *Hornem.* (Lange), *V.*

uliginosum *L.* var. *microphyllum* *Lange* (Warming), *V. Oxycoccus L.* (Warming). *Cassiope hypnoides* *Don* (Warming).

Oleaceae.—*Sp. of Jasminum* (Treviranus).

Lentibulariaceae.—*Pinguicula lusitanica L.* (Henslow).

Boraginaceae.—*Cerinthe aspera Roth* (Comes). *Asperugo procumbens L.* (Knuth).

Solanaceae.—*Petunia nyctaginiflora Juss.* (Comes). *Nicotiana Tabacum* (Darwin), *N. rustica L.*, *Hyoscyamus albus L.* (Comes). *Solanum tuberosum*, many cultivated varieties (Gard. Chron., London, xiv, 1880, p. 115).

Gentianaceae.—*Gentiana Andrewsii* (Asa Gray).

Scrophulariaceae.—*Verbascum Thapsus* and *V. Lychnitis* (Darwin), *V. phlo-moides L.* (Comes). *Celsia coromandelina Vahl* (Comes). *Scrophularia pere-grina L.* (Comes). *Vandellia nummularifolia* (Darwin). *Veronica agrestis* (Darwin). *Euphrasia Odontites* and *E. officinalis* (Darwin). *Calceolaria* (Darwin). *Mimulus luteus* (Darwin). *Collinsia bicolor Benth.* (Delpino), *C. verna Nutt.* (Delpino). *Pedicularis lanata Cham.* and *P. hirsuta L.* (Nathorst). *Antirrhinum majus*, *peloric* form (Darwin).

Labiatae.—*Ajuga reptans* (Darwin). *Salvia Horminum* (Hoffmann).

Primulaceae.—*Primula mollis* (Darwin). *Centunculus minimus* (Ascherson).

Chenopodiaceae.—*Chenopodium ambrosioides* (Hildebrand). *Beta vulgaris* (Darwin).

Bromeliaceae.—*Billbergia zebrina* (Fr. Müller).

Orchidaceae.—*Ophrys apifera* and a few other Orchids (Darwin).

Scitaminaceae.—*Hedychium coronarium* (Fr. Müller). *Alpinia sp.* (Fr. Müller).

Liliaceae.—*Allium Cepa* (Darwin).

Iridaceae.—*Marica sp. al.* (Fr. Müller). *Cypella sp.* (Fr. Müller). *Gladiolus sp.* (Treviranus). *Trimeriza sp.* (Fr. Müller).

Marantaceae.—*Canna Warscewiczii* (Darwin). *Thalia dealbata Desf.* (Pedicino).

Gramineae.—*Zea Mays* (Darwin, Knuth). *Sp. of Festuca, Poa, and Bromus* (Beijerinck). *Avena sativa* (Hoffmann). *Triticum vulgare L.* (Rimpau, Hoffmann), *T. turgidum* (Hoffmann), *T. monococcum L.* (Beijerinck). *Hordeum vulgare* and *trifurcatum* (Hoffmann).

Further contributions to our knowledge of self-fertile plants are given (cf. Loew, 'Einführung,' p. 314) by: Th. Meehan (Proc. Acad. Nat. Sci., Philadelphia; Nature; Pub. Univ. Pa. Sci. Bot., Philadelphia; The Amer. Nat., Boston; Bot. Gaz., Chicago; Bull. Torrey Bot. Cl., New York, &c.), Caruel (Nuovo Giorn. bot. ital., Firenze, x, 1878), A. S. Wilson (J. Bot., London, New Series, iv, 1875; Trans. and Proc. Bot. Soc., Edinburgh, xi and xii, 1873-4), G. Henslow (Nature, xiv, 1876; Trans. Linn. Soc., London, Series 2, i, 1877; Pop. Sci. Rev. xviii, 1879), &c. The observations published in these works are so numerous that they cannot here be dealt with individually, but reference must be made to the original works.

III. Geitonogamy.

Kerner, in his paper 'Die Schutzmittel der Blüte,' was the first to distinguish between Geitonogamy and Xenogamy. According to the few experiments of Darwin ('The Effects of Cross- and Self-fertilisation') and of Hildebrand ('Geschlechterverteilung,' pp. 67, 68) it appears, as was to be expected, to be less advantageous for the plant than Xenogamy, but considerably more advantageous than Autogamy. Geitonogamy is brought about not only by atmospheric currents and the agency of insects, but also by mature stigmas coming into contact with the pollen-covered anthers of neighbouring flowers, or by the fall of pollen. Kerner gives a full account of these two latter kinds of Geitonogamy in his 'Nat. Hist. Pl.' (Eng. Ed. I, II, pp. 318-31).

According to this investigator the significance of crowded inflorescences (Compositae, Umbelliferae, &c.), lies chiefly in the crossing that results between neigh-

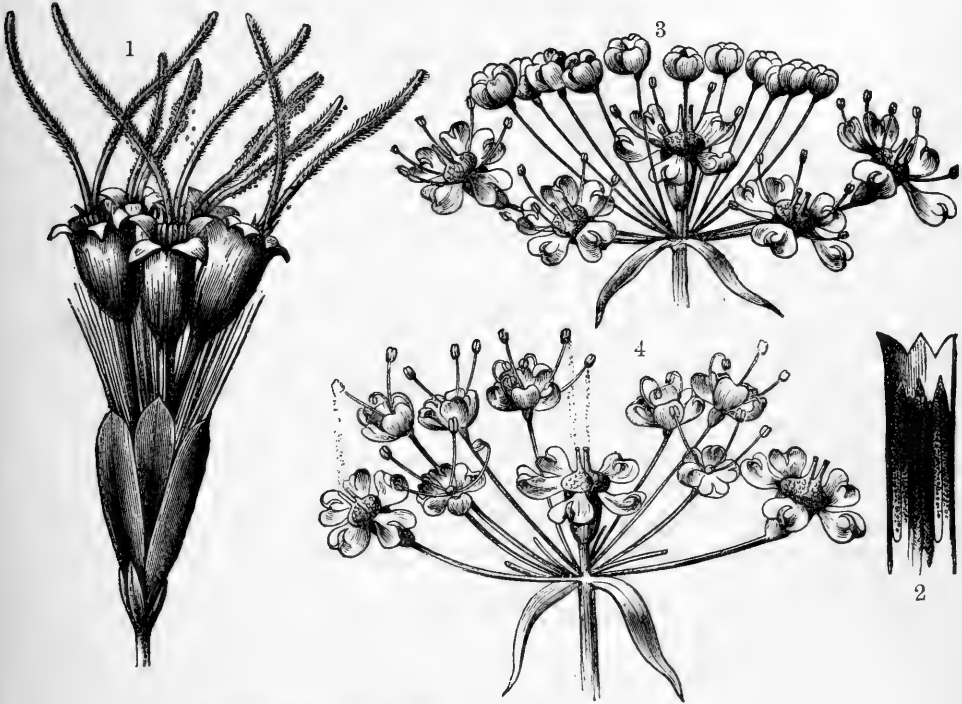


FIG. 2. *Geitonogamy with adhesive pollen* (after Kerner). (1) Crossing of branches of the styles of adjacent florets in the capitulum of *Eupatorium cannabinum*. (2) Longitudinal section through the upper parts of a young floret of *Eupatorium*: the two branches of the style lie parallel to one another, enclosed in the anther-cylinder, which is again surrounded by the corolla-tube. (3) Umbellule of *Chaerophyllum aromaticum*: the true hermaphrodite florets are open, the pseudo-hermaphrodite pollen-florets still closed. (4) The same umbellule: the true hermaphrodite florets are now without stamens, the pseudo-hermaphrodite florets are open, pollen is dropping from the anthers of the latter upon the stigmas of the former.

bouring flowers of the same plant. In numerous Compositae belonging to the group Liguliflorae, the spreading branches of the stigmas of adjacent florets intertwine at the end of the period of maturity, so that pollen entangled in the hairs of the style-branches comes into contact with the papillated stigmatic surfaces of the neighbouring florets. Geitonogamy is also favoured by the fact that the capitula close

in the evening. Among Tubuliflorae, Geitonogamy is comparatively rare. In *Eupatorium cannabinum* (see Fig. 2), and in other species of this genus, the branches of the stigmas of the older florets of a head separate so widely that they touch the pollen-covered hairs of the neighbouring florets, which are just beginning to open. In *Tussilago*, when the head closes in the evening, the pollen emptied out of the anther-tubes of the disk-florets is transferred to the ligulate ray-florets. When the head opens again, the pollen slides down the ligulate corollas to the stigmas situated at their bases. In *Calendula*, the style-branches of the ligulate ray-florets curve over the pollen-covered disk-florets, and thus get pollinated. In the Asterineae (*Aster*, *Solidago*, &c.) the pollen of the disk-florets falls on to the already mature stigmas of the ray-florets, in consequence of the inclination of the heads. In many Compositae (*Homogyne*, *Artemisia*, *Doronicum*, *Senecio*, *Telekia*, *Bupthalmum*, *Anthemis*, *Matricaria*, and others) the branches of the stigmas curve back like a bow, so that the pollen clinging to the hairs of the style reaches the stigmatic surfaces of the older adjacent florets. This is rendered particularly easy in these flowers by the fact that the torus is arched, so that the inner and younger florets (which are covered with pollen) are necessarily at a higher level than the outer and older ones, which are already in the female condition.

Among Umbelliferae the arrangements leading to Geitonogamy are scarcely less varied than in Compositae. Kerner (op. cit., pp. 323-5) describes the arrangements in question present in *Eryngium*, *Astrantia*, *Sanicula*, *Laserpitium*, *Pachypleurum*, *Siler*, *Athamanta*, *Meum*, *Chaerophyllum* (see Fig. 2), *Anthriscus*, *Foeniculum*, *Coriandrum*, *Sium*, *Ferulago*. Kerner further mentions that these may serve as types for numerous plants of other families, of which the flowers are crowded together in heads, clusters, corymbs, spikes, or racemes; especially among the Cornaceae, Caprifoliaceae, Rubiaceae, Scrophulariaceae, Rosaceae, Polygonaceae, Liliaceae, Aroideae. He subsequently describes the Geitonogamy of *Calla palustris*, *Saxifraga juniperifolia*; *Veronica maritima*, *spicata*, and *spuria*; *Eremurus caucasicus*, *Allium victorialis*, *Polygonum Bistorta*, *Rheum*, *Rumex alpinus*; *Thalictrum alpinum*, *foetidum*, and *minus*; *Erica carnea*, *Lathraea squamaria*, *Clandestina rectiflora*, *Bartsia alpina*, *Crucianella stylosa*. These relations are briefly described in the second volume of my work in dealing with floral adaptations, so far as the plants named by Kerner belong to the European Flora.

IV. Xenogamy.

Reference has already been made in the historical part to the significance of Xenogamy, which was first recognized by Darwin, as well as to the modification by Hermann Müller of the resultant Knight-Darwin law. It occurs not only among diclinous plants, but also in most monoclinal plants, since, in the latter, male and female floral stages are brought about by Dichogamy. As already mentioned in the synopsis of floral arrangements (p. 29) only cross-pollination is possible in such cases, for as stamens and carpels mature at different times, the stigmas have shrivelled up by the time the anthers dehisce, or vice versa. In plants where Dichogamy is not so well marked cross-pollination predominates at first, but self-pollination later on becomes possible.

The discoverer of Dichogamy (Sprengel, 'Entd. Geh.,' p. 19) named the two cases of this phenomenon male-female (Androgyna), and female-male (Gynandra). These two technical terms cannot, however, be used here, since Linnaeus employed them in other connections. Hildebrand, in 1867 ('Geschlechterverteilung,' p. 16), introduced the expressions Protandry and Protogyny, which would have been universally accepted by botanists as being suitable, had not the forms Proterandry and Proterogyny, employed by Delpino in 1868 and 1875 ('Ulteriori osservazioni,' i and ii), been still more widely adopted. Kirchner, in 1888 ('Flora von Stuttgart,' p. 39, note), called attention to the fact that Hildebrand's terms are preferable because shorter and more convenient, while grammatically quite as correct as those of Delpino¹.

Dichogamy is by no means limited to individual flowers, for probably all monoecious and most dioecious plants are dichogamous. All the former appear to be protogynous, i. e. the female flowers of a plant mature before the male, and this time-difference in the development of the sexes often amounts to several days. Thus, the female flowers of *Alnus viridis* are mature four or five days before the male, those of *Typha minima* as much as nine days, while according to Kerner ('Nat. Hist. Pl.,' Eng. Ed. I, II, p. 313), in the case of alders, birches, elms, oaks, beeches, hazels, planes, and the walnut, the difference amounts to two or three days. According to my own observations, the difference, especially in the case of *Corylus avellana*, may be much greater under certain circumstances. If, in particular, an unfavourable rainy or cold period sets in, after the protrusion of the stigmas, the discharge of pollen is considerably delayed.

Most dioecious plants are also protogynous. According to Kerner (op. cit.) the female flowers of many willows are mature several days before the male, in spite of the fact that the male trees are subject to the same conditions of life as the female; they grow in the same ground, are exposed equally to sunlight, and encounter the same currents of air. Again, according to Kerner, the stigmas of the female flowers of *Salix amygdalina* are ready for pollination two or three days before the anthers of the male flowers dehisce. The same holds for *S. purpurea*, *viminalis*, and *fragilis*, while the willows of the lower Alps (*S. herbacea*, *retusa*, and *reticulata*) usually present a difference of one day only in the development of the two kinds of flowers. In *Cannabis sativa*, the difference amounts to four

¹ As these terms will be much used in botanical instruction in secondary schools, efforts have been made to find suitable German equivalents for them. W. Behrens in the first edition of his 'Lehrbuch der Allgemeinen Botanik' spoke of 'männlich-weiblich' (male-female) (♂-♀) and 'weiblich-männlich' (female-male) (♀-♂) ways of flowering, thus making use of Sprengel's original terms. [The latter symbol is the long-recognized one for *monoecious* and is incorrectly introduced in the sense of the text by Behrens, and reproduced in the English edition of his textbook.—ED.] He retained these expressions in his second edition (1882, p. 182), but in the third edition of his textbook he introduced 'vormännlich' and 'vorweiblich' [i. e. male first and female first], as proposed by Hildebrand. E. Nichel (Bot. Centralbl., Cassel, xlix, 1892, pp. 10, 11) suggested the terms 'pollenvorreif' or 'narbennachreif' [i. e. pollen first ripening or stigma last ripening], and 'narbenvorreif' or 'pollennachreif' [i. e. stigma first ripening or pollen last ripening], and for monogamous the term 'zwitterreif' [i. e. bisexual ripening]. I would replace these (op. cit., lii, pp. 217, 218) by the terms 'staubblattvorreif' and 'fruchtblattvorreif' [i. e. stamen first ripening and carpel first ripening], but at the same time maintain that the terms Proterandry and Proterogyny should be applied as a matter of course by scientific botanists, and as international terms. [In Britain the scientific terms protandry or proterandry and protogyny or proterogyny are in general use.—ED.]

or five days; in *Humulus Lupulus*, *Mercurialis perennis*, and *ovata*, and others, it is at least two days.

Those plants which bear falsely hermaphrodite flowers behave just like the true diclinous plants. Such flowers possess both stamens and pistil, and look like genuine hermaphrodites, but either the anthers are degenerate, containing no pollen capable of fertilizing (falsely hermaphrodite fruiting-flowers) or the pistil does not come to maturity (falsely hermaphrodite pollen-flowers). According to Kerner (op. cit., pp. 312-13) various Valerians (*Valeriana dioica*, *polygama*, *tripteris*) living in the same localities open their falsely hermaphrodite fruiting-flowers three to five days earlier than their falsely hermaphrodite pollen-flowers, so that they are markedly protogynous. In *Rumex alpinus*, the difference amounts to two or three days; in *Fraxinus excelsior* usually to four days, and in numerous grasses (*Anthoxanthum odoratum*, *Hierochloa australis*, *Melica altissima*, *Sesleria coerulea*) to two days.

In Homogamous open flowers cross-pollination is also predominant in most cases, at least at first. This is either because the pollen surrounding the stigma is ineffective for the fertilization of the same flower (see the list of self-sterile plants, p. 36), or the anthers lie, at any rate to begin with, deeper than the stigma (many Cruciferae), or they are remote from the stigma (Sileneae), or they turn the dehiscent side outwards (many Cruciferae). Numerous interesting cases illustrating the impossibility of self-pollination, or at least of its restrictions, are presented by the floral adaptations of Orchidaceae, Iridaceae, Violaceae, Ranunculaceae, Labiatae, Scrophulariaceae, Boraginaceae, Asclepiadaceae, and Apocynaceae. An account of them is impossible here, and reference must be made to the second part of this handbook, in which the floral adaptations of individual species are fully described.

Delpino ('Ult. oss.' Atti Soc. ital. sc. nat., Milano, xvi, pp. 332 et seq.) distinguishes four degrees of **Herkogamy**.

1. **Absolute Herkogamy** (Ercogamia assoluta): the transference of pollen to the stigma can only be effected by animals; the possibility of self-pollination is always excluded.

2. **Contingent Herkogamy** (Ercogamia contingente): here, too, the visits of insects are necessary for pollination, but accidental self-pollination is not excluded.

3. **Half-Herkogamy** (Emiercogamia): the flowers are at first absolutely herkogamous. If there are no insect-visits at this time, self-pollination takes place in the second stage of flowering, being rendered possible from growth or change in position of the parts of the flower.

4. **Concealed Herkogamy** (Ercogamia oscura): the herkogamy is inconspicuous. When insects visit the flowers self-pollination can take place as easily as cross-pollination. Failing such visits self-pollination is spontaneously effected.

V. Heterostyly.

In speaking of the flowers of *Hottonia palustris* ('Entd. Geh.,' p. 103) Sprengel says:—'Some plants have only flowers of which the stamens are included in the corolla tube, while the style projects from it; and other plants have only flowers with the style shorter, but the stamens longer than the corolla tube.'

I do not think that this is a chance arrangement, but an adaptation of Nature, though I am not now in a position to indicate the object of it.' Sprengel was therefore acquainted with Dimorphism¹, but its significance was first made clear by Darwin (see p. 8). Vaucher was the first to observe the Trimorphism of *Lythrum Salicaria* (1841, Hist. phys. des plantes d'Europe, II, p. 341), and it was afterwards noticed by Wirtgen (Verh. d. naturh. Ver. für Rheinl. und Westfalen, v, 1848, p. 7).

In the large majority of cases Heterostyly is associated with other differences between the two forms of flower than unequal length of style and stamens. In dimorphous flowers, for example, the pollen-grains of the long-styled flowers are considerably smaller than those of the short-styled ones, while the stigmatic papillae of the former are considerably longer than those of the latter.

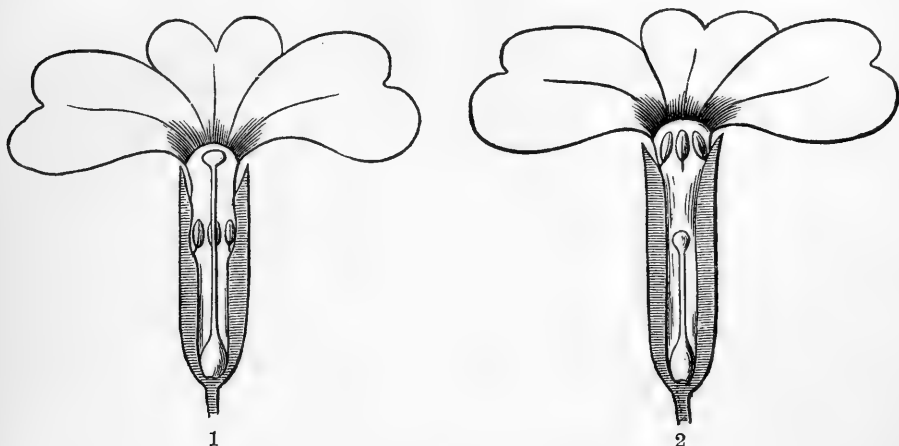


FIG. 3. *Primula acaulis*, Jacq., a plant with dimorphous flowers. (Longitudinal section) twice natural size.

(1) Long-styled form.

(2) Short-styled form.

0

3

0

4

Relative sizes of pollen-grains—

(3) Of the short-styled form.

(4) Of the long-styled form.



5



6

Relative sizes of stigmatic papillae—

(5) Of the long-styled form.

(6) Of the short-styled form.

[(3)-(6) Highly magnified.]

In some cases of dimorphism there is also a noticeable dissimilarity between the two forms of flower in regard to size and conspicuousness. The long-styled flowers of *Primula longiflora* and *minima*, for example, possess a larger and more conspicuous limb to the corolla than the short-styled, while in *Primula auricula* and *glutinosa* the opposite is the case. In the former two species the short-styled flowers are capable of self-pollination, as are the long-styled ones of the other two. Kerner, after

¹ According to Loew, 'Einf. in d. Blütenbiologie' (p. 55, note), Dimorphism was discovered almost simultaneously by Sprengel, W. Curtis ('Flora Londinensis,' I. Edit. 1777-87), and Persoon (Usteri's Annalen, 1794, Part 2). The last two both made the discovery in *Primula*.

mentioning these examples, goes on to say ('Nat. Hist. Pl.,' Eng. Ed. I, II, p. 396):— 'It may be taken to be a general rule that the flowers adapted to cross-fertilization in which no autogamy takes place are larger than those in which the accomplishment of autogamy is assured. This phenomenon has been explained by the circumstance that flowers destined to be crossed with others require to be more plentifully equipped with the means of attracting insects than those which are certain to undergo pollination even if no insects visit them.'

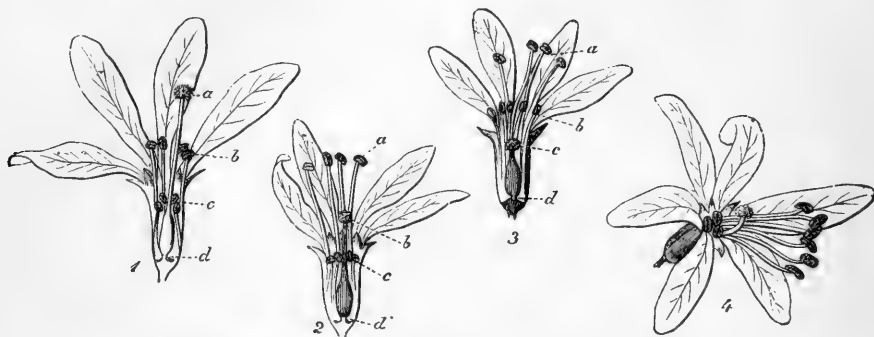


FIG. 4. *Lythrum salicaria*, L. (after Herm. Müller). (1) Long-styled flower. Seen from above, after removal of the upper third of the calyx, corolla, and stamens. (2) Flower with style of medium length similarly treated. (3) Flower with short style similarly treated—*a*. Long stamens and style. *b*. Medium stamens and style. *c*. Short stamens and style. (4) Flower with medium style seen obliquely from the right front.

Trimorphous flowers differ from one another in similar ways to the dimorphous, as regards size of stigmatic papillae, pollen-grains, and the like. In the typical trimorphic plant *Lythrum Salicaria*, the pollen-grains of the long stamens are the largest, those

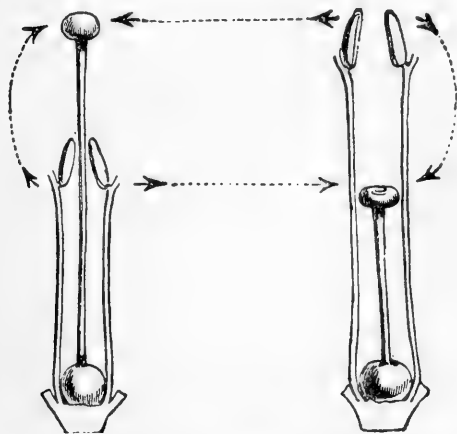


FIG. 5. Diagram of the possible legitimate and illegitimate unions in a dimorphic plant (*Primula*) (after Darwin). The arrows indicate the anthers from which pollen must be brought to the stigma of either of the two forms, so as to give a legitimate union (the straight horizontal lines), or an illegitimate union (the curved lines on right and left). (Loew.)

of the medium stamens are of intermediate size, and those of the short stamens the smallest; the anthers of the long stamens are green, those of the medium and short are yellow; the filaments of the long stamens are red, those of the medium and short are green; the stigmatic papillae of the long-styled flowers are noticeably longer than those of the medium, and these are a little longer than those of the short-styled; the seeds of long-styled flowers are larger than those of medium-styled flowers, and these again are larger than those of short-styled flowers.

Epigaea, according to Asa Gray, has even tetramorphous flowers, differing from one another partly in the length of the style, partly in regard to the stigma and anthers.

Among dimorphous flowers four modes of fertilization are possible, two of them legitimate, and two illegitimate. Darwin has represented the possible legitimate and illegitimate unions by the accompanying diagram (Fig. 5).

Eighteen modes of fertilization are possible among trimorphous flowers, and of these six are legitimate. If we indicate the longest organs (δ and φ) by l , the medium ones by m , and the shortest by s , and use a , b , and c to represent the long-styled, medium-styled, and short-styled forms respectively, the six legitimate crossings possible are as follows:—

$l \delta (b)$ with $l \varphi$.	$m \delta (a)$ with $m \varphi$.	$s \delta (a)$ with $s \varphi$.
$l \delta (c)$ „ $l \varphi$.	$m \delta (c)$ „ $m \varphi$.	$s \delta (b)$ „ $s \varphi$.

The twelve illegitimate modes of crossing are:—

$l \delta (b)$ with $m \varphi$.	$m \delta (a)$ with $l \varphi$.	$s \delta (a)$ with $l \varphi$.
$l \delta (b)$ „ $s \varphi$.	$m \delta (a)$ „ $s \varphi$.	$s \delta (a)$ „ $m \varphi$.
$l \delta (c)$ „ $m \varphi$.	$m \delta (c)$ „ $l \varphi$.	$s \delta (b)$ „ $l \varphi$.
$l \delta (c)$ „ $s \varphi$.	$m \delta (c)$ „ $s \varphi$.	$s \delta (b)$ „ $m \varphi$.

The six legitimate modes of crossing have been schematically represented by Darwin in the following manner:—

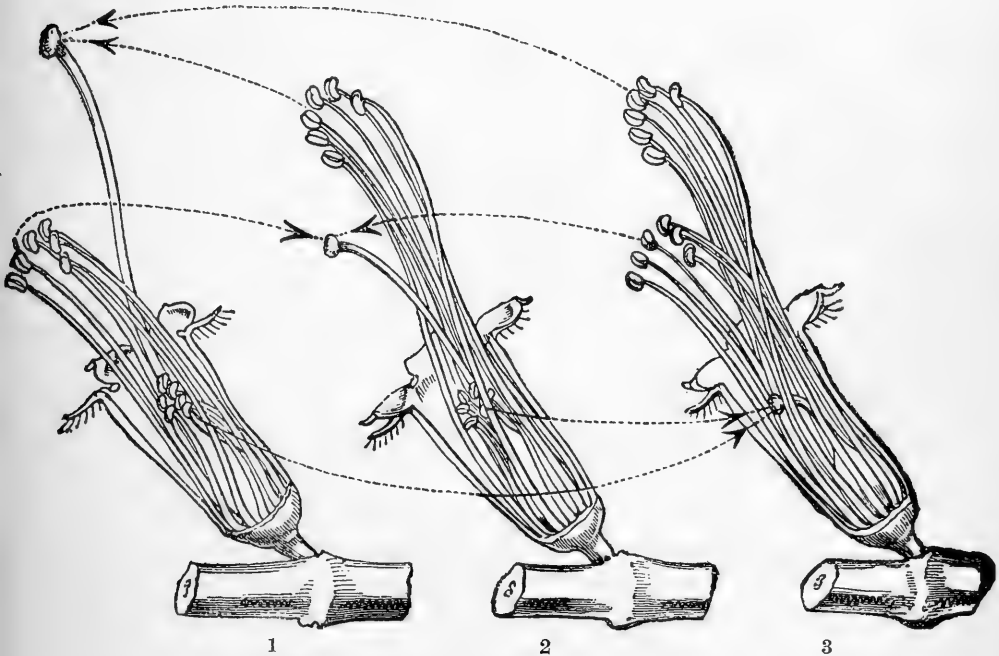


FIG. 6. Diagram showing the possible legitimate unions in a trimorphic plant (*Lythrum Salicaria*) (after Darwin). The arrows and dotted lines indicate the anthers from which the pollen must be brought to the stigma of one of the three forms, so as to give a legitimate union with complete fertility (Loew). (1) Long-styled form. (2) Medium-styled form. (3) Short-styled form.

The results of numerous experiments carried out with the greatest care by Darwin and Hildebrand are as follows (according to Loew, 'Einführung in die Blütenbiologie,' pp. 218–20):—

1. The legitimate unions usually brought about by the normal flower-visitors yield, almost without exception, a larger quantity of seed than illegitimate unions.

2. The difference as to fertility between legitimate and illegitimate unions varies in different species. Within the same genus there are some species in which illegitimate unions are almost entirely sterile (*Oxalis Valdiviana*, *O. Regnelli*), as well as others in which they are comparatively fertile (*O. speciosa*).

3. The various legitimate unions vary among themselves in respect of fertility, either to a small extent only (*Oxalis Valdiviana*, *O. Regnelli*) or in a higher degree (*Lythrum Salicaria*). Among dimorphous plants the union of short-styled forms with pollen from long-styled ones is as a rule the more fertile, but the opposite is true for *Hottonia* and *Primula acaulis*. Among trimorphous species the relations are yet more varied: in the case of *Lythrum Salicaria* the legitimate unions of the medium-styled form are the most prolific. Then comes, as regards seed production, the long-styled form, and last of all the short-styled form. In other trimorphous species, e.g. *Oxalis speciosa*, the sequence is not the same, and the differences between the several cases are not so great as in *Lythrum*.

4. Among the illegitimate unions of dimorphous species, those of the long-styled form are as a rule more fertile than those of the short-styled one (except, e.g., *Pulmonaria*, where Hildebrand found that both illegitimate unions were quite sterile). The illegitimate unions of a trimorphous species present relatively greater differences than those of dimorphous species. In *Lythrum Salicaria*, e.g., the illegitimate unions of the medium-styled form are conspicuously fertile, while, on the contrary, those of the other two forms are very infertile. According to Darwin, the infertility is here directly proportionate to the difference in length between the pistil and the filaments of the stamens which furnish the pollen for fertilization. In *Oxalis speciosa* some illegitimate unions of all three forms are fertile to a certain degree, but those of the medium-styled flowers are not more fertile than the rest.

Correns has pointed out that F. Delpino suggested an explanation ('*La Distribuzione dei sessi nelle piante*,' 1867, p. 17) of the difference between the two forms of dimorphous heterostylic flowers as to the size of their pollen-grains. His view was that the greater volume of the pollen-grains of the short-styled flowers ($\sigma +$)¹ has reference to the longer distance that the pollen-tubes have to travel in cases of legitimate fertilization, while the pollen-grains of the long-styled flowers ($\varphi +$)¹ are smaller because their tubes have a shorter distance to travel in legitimate fertilization.

Charles Darwin ('*Forms of Flowers*,' pp. 250 et seq.) has likewise given no sufficient answer to this question. He was not ignorant of the fact that difference in size of pollen-grains does not appear in all dimorphous heterostylic flowers (e.g. species of *Linum*), and that, conversely, when there is marked difference of size in the pollen-grains there may be very slight differences as to length of styles (e.g. *Sutera*). Darwin supposed that the pollen-grain is sometimes nourished by the tissue of the style.

Hermann Müller ('*Wechselbeziehungen*,' p. 86) regards the difference in size of the pollen-grains as an adaptation to the length of the style, and even recognizes

¹ The + sign is used to suggest the larger pollen-grains and longer style, respectively.—Tr.

in it the reason for the illegitimacy of some crossings:—‘Since by further natural selection the size of the pollen-grain has been adapted to the distance to be traversed by the pollen-tube in legitimate crossing, and the stigmatic papillae have been adapted to the size of pollen-grain they have to receive, it follows that sexual organs standing at dissimilar heights would be unsuited for one another, and so the illegitimate crossings of heterostylous flowers would be unfruitful.’

C. Correns remarks (Ber. D. bot. Ges., Berlin, vii, 1889) that according to this view there should really be three kinds of legitimate fertilization, i. e. $\delta +$ with $\varphi +$, $\varphi +$ with $\delta +$, and $\delta +$ with $\delta +$; but only one kind of illegitimate fertilization, i. e. $\varphi +$ with $\varphi +$. Strasburger also (Jahrb. wiss. Bot., Leipzig, xvii, 1886, p. 84) points out that the illegitimate crossing of long-styled flowers among primroses (in which the small pollen-grain reaches the stigma of the long style) should not, on this view, be more fertile than that of short-styled flowers.

Naegeli (‘Mechan. physiol. Theorie der Abstammungslehre,’ p. 151) does not consider that the different sizes of pollen-grains result from adaptation to the length of the style, for the grains are nourished by the tissue of the style while developing pollen-tubes. He sees in the differences in size and occasionally in colour of the pollen-grains, merely an external sign of internal differentiation conditioning illegitimacy; they perhaps depend, like the length of stigmatic papillae, upon the height of insertion.

Correns (op. cit.) proved by culture-experiments with the pollen of *Primula acaulis* Jacq., that the size of the pollen-grains has nothing to do either with the distance to be traversed by the pollen-tube or with the cause of illegitimacy. The following are the most important conclusions at which he arrived:—

1. Both forms of pollen produce equally long tubes in the same time.
2. The large pollen-grains develop thicker tubes than the small ones.
3. The size of the pollen-grains is not an adaptation to the length of style to be traversed in cases of legitimate fertilization, nor is it the cause of diminished fertility in illegitimate crosses.
4. There are no differences discoverable in the capacity for absorbing nourishment or in the chemotactic irritability, such as might explain the legitimacy or illegitimacy of particular combinations.
5. The length and form of the stigmatic papillae have likewise nothing to do with the greater or less fertility of particular crosses.
6. The lengths of the stigmatic papillae may be regarded as adapted to the size of the grains, but only in the sense of facilitating their reception.

Lastly, I would mention the interesting phenomenon of homo-heterostyly in *Menyanthes trifoliata*. In Greenland, according to Warming, this otherwise always dimorphic heterostylous plant is homostylous, the stigmas being at the same level as the anthers.

A list of the heterostylous plants hitherto recognized may be added:—

Trimorphous species: some *Lythraceae*, such as *Lythrum Salicaria* (Darwin). *L. Graeferi* (Darwin), *L. virgatum*, *flexuosum*, and *maculatum* (Köhne), *Decodon verticillatus* (Köhne), *Nesaea Commers.* and *Lagerstroemia L.* (Kuhn, Darwin), the *linaceous* *Roucheria Planch.* (? Kuhn), and twenty species of the genus *Oxalis*

(Hildebrand). Among Monocotyledones, *Pontederia* alone is known to be trimorphous (Fr. Müller); Kerner, however, gives also *Colchicum autumnale*.

Connarus falcatus Bl. forms the transition between trimorphous and dimorphous plants. According to Burck (Ann. Jard. bot., Buitenzorg, vi, 1887, p. 251) the flowers of this species are trimorphous in structure, but the anthers of the inner whorl always remain closed. This same phenomenon occurs in *Averrhoa Carambola* L. *Polygonum amphibium* (Knuth, 'Bl. u. Insekt. a. d. nordf. Ins.,' p. 125), is perhaps also imperfectly trimorphous.

Dimorphous species are particularly abundant in the genus *Oxalis*, 51 being enumerated by Hildebrand; also in *Linum* (30 species according to Alefeld), and *Primula* (36 species). Other dimorphous Primulaceae are *Hottonia palustris* (Sprengel), species of *Pulmonaria* (Darwin), *Gregoria Vitaliana* (Scott), and species of *Dionysia* (Kuhn). Other dimorphous Linaceae belong to the genera *Erythroxylon*, *Reinwardtia* and *Hugonia* (Kuhn).

The family of the Rubiaceae is also rich in dimorphous plants: e.g. species of *Asperula* (Kuhn), *Knoxia* (do.), *Chasalia* (do.), *Mitchella* (Darwin, Kuhn), *Hedyotis* (Fr. Müller, Kuhn), *Ophiorrhiza* (Kuhn), *Cinchona* (do.), *Nertera* (do.), *Luculia* (Kuhn), *Pentas* (Hirn), *Otomeria* (do.), *Dirichletia* and *Pentanisia* (do.), *Bouvardia leiantha* (Bailey), *Borreria* (Fr. Müller), *Manettia* (do.), *Faramaea* (do.), *Androsacme longifolia* (Clarke), *Randia uliginosa* (do.), species of *Houstonia* (Meehan); *Psychotria aurantiaca*, *perforata*, *sarmentosa* var. *angustata*, *montana*, *robusta*, and *expansa* (Burck), *Chasalia lurida* (do.), *Cephaelis Beerii* and *Ipecacuanha* (do.), species of *Saprosma* (do.), *Serissa foetida* (do.), *Knoxia lineata* (do.), species of *Hedyotis* (do.), *Spermacoce verticillata* (do.), *Cinchona succirubra*, *Calisaya*, *Ledgeriana*, *officinalis*, and *carabayensis* (do.), *C. micrantha* (Darwin).

The family of the Turneraceae also contains numerous dimorphous species. J. Urban (Jahrb. bot. Gart., Berlin, ii, 1883) enumerates 48 completely and 6 incompletely dimorphous species. Many of the Lythraceae are dimorphous; e.g. (according to Köhne, 'Monogr. d. Lythraceen') species of the genus *Lythrum* belonging to the group *Pythagorea* (except *L. maritimum*, which is homostylous), species of *Pemphis*, *Adenaria*, *Rotala floribunda*.

Among Boraginaceae the following are dimorphous: *Pulmonaria officinalis* (Darwin, Hildebrand), *P. angustifolia* L. = *P. azurea* Bess. (Darwin), *Cordia* (Darwin), *Amsinckia* (Kuhn), *Arnebia* (Kuhn), *Lithospermum canescens* (Bessey), *Macrotomia perennis* (Clarke); among Gentianaceae the following, *Menyanthes trifoliata* (Kuhn), *Villarsia Humboldtianum* (Fr. Müller), species of *Hockinia* and *Limnanthemum* (Kuhn). Darwin, however, does not regard *Amsinckia* and *Arnebia* as dimorphous, but only as possessing stamens and styles of variable length.

Dimorphous Hypericaceae:—*Cratoxylon formosum* (Darwin, Dyer); Sterculiaceae:—*Melochia parvifolia* H. B. K. in Caracas (Ernst); Silenaceae:—*Silene petraea* (Lalanne, Caille); Rhamnaceae:—*Rhamnus lanceolatas* Pursh (Darwin); Plumbaginaceae:—Brazilian species of *Plumbago* and *Statice* (Fr. Müller), *Statice Limonium* in Belgium (MacLeod); Verbenaceae:—species of *Aegiphila* (Darwin); Santalaceae:—*Thesium intermedium* (Schulz); Amarantaceae:—*Chamissoa*, with transition to *dicliny* (Fr. Müller).

The following species are incompletely heterostylous:—*Narcissus Tazetta* var.

algerica (Battandier, Bul. soc. bot., Paris, xxx), *Brassica nigra* (Todd, Amer. Nat., Boston, xv, 1881), *Erythraea Centaurium* (A. S. Wilson, Brit. Ass. Rep., 1878), and *Anchusa officinalis* (E. Warming, Bot. Tids., Kjöbenhavn, xvii, 1877). I myself always found the last three species homostylous.

VI. Cleistogamy¹.

Hugo von Mohl in his memoir, 'Einige Beobachtungen über dimorphe Blüten' (Bot. Ztg., Leipzig, xxi, 1863, pp. 309 et seq.), mentions a number of plants bearing on the same stock some flowers that open normally and also others that do not open at all. The corolla of such flowers is reduced or absent, while stamens and pistil are in some respects well developed. Healthy fruits result from the self-fertilization that takes place in the permanently closed bud-like flowers. A few years later Kuhn (Bot. Ztg., xxv, 1867, pp. 65-7) published a further and extensive list of such plants, and introduced the term *cleistogamous* to designate the permanently closed flowers.

According to H. v. Mohl (Bot. Ztg., xxi, 1863), Dillenius was probably the first to discover cleistogamous flowers on the plant subsequently named *Ruellia clandestina* by Linnaeus (Hort. Eltham., 1732, p. 328, Fig. 320). *Viola mirabilis* was the second plant in which Dillenius observed this phenomenon: he found that the spring-flowers with well-developed corolla and fully formed reproductive organs rarely produce fruit, while the later flowers devoid of corolla do so regularly.

In many parts of his writings Linnaeus speaks of cleistogamous flowers, and proves that in these small blossoms the want of stamens and carpels is only apparent.

Our knowledge of cleistogamous flowers was further extended by the observations of:—Schkuhr, Hegetschweiler, De Candolle, Du Petit Thouars, L. C. Richard, Adrien de Jussieu, Aug. St. Hilaire, Bentham, Torrey and Asa Gray, Spach, Weinmann, Wight, Weddell, Maximowicz, Daniel Müller, Brongniart, Michalet, and others. H. v. Mohl's (op. cit., pp. 321-8) researches finally gave us a clear view of these remarkable flowers.

Hugo von Mohl's classical account of the cleistogamous flowers of *Oxalis Acetosella* (Bot. Ztg., 1863, pp. 321, 322) is somewhat as follows. In the second week of June, when the fruits of the spring-flowers possessing corollas contained ripe seeds (at Tübingen), there were large numbers of small flowers in all stages of development up to the complete maturation of fruit. They usually occurred on plants which had developed one or several spring-flowers in the axils of the upper leaves, but were also occasionally present on plants devoid of spring-flowers. These summer-flowers and fruits are distinguished very easily from the spring-flowers by the different length and direction of the flower-stalk. The stalk of the spring-fruit has a length of about three inches, is straight, and possesses a joint bearing two bracteoles, about half-way down. The peduncle of the small flower, on the other hand, is only about four lines long (1''' = about $2\frac{1}{2}$ mm.), and bent like a hook at the top, while its joint is only $\frac{1}{2}$ -1 line from the flower. The latter, owing to the shortness of the flower-stalk, is hidden in the moss and pine-needles among

¹ [See K. Goebel, 'Die kleistogamen Blüten und die Anpassungstheorie,' Biol. Centralbl., Berlin, xxiv, 1904, for the most recent exposition of cleistogamy.—ED.]

which the plant grows. The capsules of the summer-flowers are shorter and thicker than those of the spring-flowers, because the upper part of the carpels which is continued into the style, does not grow out into a long pointed process, as it does in the latter. In each chamber there are usually four seeds, just as in the fruits of the spring-flowers, and there is no difference between the seeds of the two kinds of fruit.

At the time of its full development, the summer-flower has a length of rather more than one line, and its form is that of a closed flower-bud. The tip of the white corolla projects a little between the tightly closed sepals, but without making an entrance to the interior of the flower. The corolla consists of five ovate petals, with twisted aestivation, so as to closely envelop the essential organs. The five outer stamens are about half as long as the ovary, and their anthers are extremely small; the five inner stamens possess far larger anthers, and some of them attain the length of the ovary, while others are rather shorter than this. The five very short styles are therefore situated either right in the middle of the larger anthers, or project a little beyond them. The small size ($1/8$ th– $1/9$ th line = 0.21–0.25 mm.) of the inner anthers is associated with a correspondingly small quantity of pollen, and the number of pollen-grains in each loculus may not exceed two dozen, while in the still smaller anthers of the outer stamens there are not more than a dozen. In spite of the relative fewness of the grains in comparison with other flowers, the amount of pollen is really not inconsiderable in relation to the number of the ovules to be fertilized, having regard to the fact that owing to the complete closure of the flower none of it can be lost, and considering how fertilization is furthered by the proximity of anthers and stigmas. The pollen-grains are not dehiscent, but germinate while still enclosed in the anthers. The pollen-tubes grow out in an irregular tangle from both sides and from the tips of the anthers. They creep here and there among the anthers and styles, and for the most part climb up the latter to reach the small stigmas. The anthers are bound together and united with the stigmas by the pollen-tubes.

The process of fertilization appears to be quickly accomplished, for comparatively few flowers are found in the stage of development just described. When the corolla, still closely twisted, protrudes more obviously beyond the tips of the sepals, owing to the swelling up of the ovary, the anthers are already withered, and hang from the stigmas, having been detached from the persistent filaments. If the anthers are softened and opened at this stage, the pollen-grains will still be found enclosed in them.

In *Impatiens Noli-tangere* the arrangements are very like those of *Oxalis Acetosella*. At the time of their full development the small flowers have the form of a closed, elongated bud about one line (about $2\frac{1}{4}$ mm.) in length, the upper part of the closely overlapping sepals, which projects beyond the sexual parts, being contracted into a relatively thin, blunt, conical process. The petals in the form of whitish scales of the same length as the pistil, and the anthers, which are carried on relatively long filaments, are inclined towards one another, so as to form a hood above the pistil, but they are not united to one another. When the ovary elongates after fertilization, it carries up the whole united mass of sepals, petals, and stamens in the form of a small cap, like the calyptra of a moss capsule.

At the time of fertilization the ovary is 0.75–0.8 of a line (about 2 mm.) in length, and crowned by five very short conical pointed styles, ending in punctate stigmas. The anthers have a triangular connective, with apex above, over which the small loculi (0.24 of a line in length) project. The number of pollen-grains developed in each loculus does not exceed forty, or at most fifty. They are ovoid, about 0.015 of a line in length, and 0.01 of a line in breadth (=0.03 and 0.02 mm.), and are colourless. Although the anthers dehisce markedly, the pollen-grains escape no more than they do in *Oxalis*, but, as in the latter, germinate within the anthers, with the production of very numerous pollen-tubes, which unite the anthers with the stigmas. These tubes are very soft, so that they tear when the anthers are pulled away, without drawing the pollen-grains out of the loculi.

In *Specularia perfoliata* there is a small whitish mound in the basin-shaped depression of the superior calyx, which, looked at through a lens, is seen to be traversed by prominent radiating ridges, from which several (some 6–12) small bristles project. In this mound the stamen and styles are concealed. Their number and relative position are easily recognized when the upper part of the mound is removed by a transverse cut. It is then seen to be hollow, its wall consisting of a very thin membrane. The stamens come into lateral contact with one another above the tips of the styles. Their number corresponds to that of the calyx lobes, 3–5. The number of the styles and chambers of the ovary is usually two when the calyx lobes are three or four, and three when the calyx lobes are five.

The whitish membrane that forms the mound in question corresponds undoubtedly to the corolla, but there is no trace of a division into separate lobes or of any opening in the middle of the mound. The form of the cavity enclosed by the corolla changes as the flower develops. In very small flowers that are as yet far removed from the stage of fertilization, the corolla appears as a moderately sharp cone, but this becomes more and more flattened with the growth of the ovary. While the upper part of the cavity that contains the stamens and style thus diminishes in size, at least relatively, the under part increases, since it assumes the form of a funnel projecting into the ovary. The actual size of this cavity, however, is always very limited. The filaments of the stamens inserted at the periphery of this cavity are very short; the anthers measure about 0.13''' (about 0.3 mm.) in length. They are colourless, and contain a considerable quantity of pollen-grains. These are without colour, and their diameter is 0.014''' to 0.017''' (about 0.035–0.044 mm.). The styles are relatively thick, and of ovoid form; their tips and their inner sides are stigmatic. There is no trace of the characteristically formed collecting-hairs that are always present on the outer sides of the styles of *Campanulaceae*. The pollen is not scattered, but spreads its tubes from the anthers. They take an irregular course through the space that exists between the anthers and styles, as well as laterally between the anthers themselves. These organs are thus united together with moderate firmness, so that their upper part can be cut away by a vertical section without causing displacement. The pollen-tubes are so tough that many of them are not torn across if the anthers are pulled away from the styles, but remain connected

with the stigmas by their extremities, and the pollen-grains from which they spring are drawn out of the anthers.

As previously shown by the researches of Dan. Müller, there are a few slight modifications of the process of fertilization in various species of *Viola*, for here the pollen-grains do not remain enclosed in the anthers under all conditions.

I should like to add to these descriptions of H. v. Mohl that the cleistogamous flowers of species of *Drosera* are very well adapted for observations on the phenomena that have just been considered.

In *D. rotundifolia* (at Kiel) open flowers are extremely rare; as a rule, only buds, bud-like flowers, and fully formed fruits are found on an inflorescence. The youngest buds of about $1\frac{1}{2}$ –2 mm. in length are best suited for orientation. In these the moderately coarse green sepals and also the very delicate white petals are readily detached, exposing the ovary with its three or five short, curved styles, which bear terminal stigmas in the form of small swellings. The stamens are closely applied to the ovary, and are of such a length that the pale two-chambered anthers occur at about three-fourths of its height. (Cf. Fig. 7.)



FIG. 7. Cleistogamous Flower of *Drosera rotundifolia* L., before the formation of pollen-tubes. Sepals and petals have been removed. $\times 12$ approximately. (From nature.)

In flowers that are further developed it is more difficult to obtain a knowledge of the relations, owing to the fact that the pollen-grains have produced their tubes in the form of fine white threads which have become so firmly attached, not only to the stigmas but also to the petals, that when an attempt is made to remove the floral envelopes, the anthers are torn out of their place. Owing to this I have not succeeded in opening flowers in which fertilization was going on, without disturbing the position of the essential organs, and tearing the filaments from their insertions.

When the flowers reach a length of 3 mm. they are already fertilized, and the white petals, which are united to the withered anthers by pollen-tubes, begin to grow out between the previously closed tips of the sepals, owing to the increased size of the carpels, much as in *Oxalis* and *Impatiens*. The corolla, previously enclosed by the calyx and which thus becomes externally visible in the form of a whitish point, next withers, so as to look like a brown speck on the top of the ovary, which goes on elongating as the seeds mature, and continues to be surrounded by the persistently growing calyx¹.

¹ The explanation of the predominance of cleistogamy in the sundew may be found in the circumstance that the small flying insects which could effect cross-fertilization are attracted by the glistening drops on the numerous glandular hairs of the leaves, to such an extent that they make no attempt at cross-pollination, but fly to the hairs. Owing to the continual capture of insect-prey open flowers are useless for the sundew, and it therefore develops cleistogamous ones.

In the case of our other plants with cleistogamous flowers the conditions are different: in *Oxalis* the cleistogamous flowers develop only in June and July, at a time when numerous other flowers attract the cross-pollinating insects, which would pay little attention at that time to the concealed and quite inconspicuous flowers of this plant. In spring, on the other hand, open flowers are formed, because then the competition among the flowers has not become so great, and insects are attracted even by the flowers of the wood-sorrel. The same holds true for species of violet (e.g. *Viola mirabilis*), which 'bloom unseen.' General rules regarding the appearance of cleistogamous flowers cannot be deduced from these examples, but each case must be studied separately.

Lamium amplexicaule develops cleistogamous flowers twice a year, i.e. in spring, before the chasmogamous forms appear, and in autumn, when the weather has become cooler. Here again the pollen-grains in the closed flowers send out their pollen-tubes to the stigma, either after escaping from dehiscent anthers or while still in anthers that remain closed; in the latter case the pollen-tubes break through the anther-wall. In this case also good fruits are developed.

According to Hildebrand ('Geschlechterverteilung,' p. 77), many flowers pollinate and fertilize themselves cleistogamously under water, in cases where this is so deep that the flowers cannot reach the surface. This occurs, e.g., in *Ranunculus aquatilis* (Axell), *Alisma natans*, *Illecebrum verticillatum*, *Subularia aquatica* (Axell), and others. Hansgirg (Bot. Centralbl., Cassel, xlv, 1891, pp. 74, 75) distinguishes such flowers as *pseudo-cleistogamous*, as contrasted with genuinely cleistogamous ones. They completely agree with normal open flowers as regards size, form, position, &c., and like them possess all the specializations that serve for attracting insects.

In certain circumstances therefore the otherwise normally opening chasmogamous flowers remain closed, and fertilize themselves. This may be brought about: 1. In consequence of deficiency of light,—*photo-cleistogamous* flowers (*p*); 2. in consequence of high water-level, or strong current, owing to which the flowers remain closed under water,—*hydro-cleistogamous* flowers (*h*); 3. in consequence of insufficient warmth,—*thermo-cleistogamous* flowers (*t*).

Hansgirg (op. cit.) gives a list of all the pseudo-cleistogamous flowers known to him, viz.:—

Ranunculaceae: *Ranunculus aquatilis* (*h*).

Nymphaeaceae: *Nymphaea coerulea*, *N. zanzibariensis*, *N. madagascariensis* (*p* or sometimes *h*), *Victoria regia* (ditto), *Euryale ferox* (ditto).

Portulacaceae: *Montia fontana* (*p* or sometimes *t*).

Caryophyllaceae: *Stellaria media* and var. *pallida* (*S. Boraeanae*), *S. cerastoides*, *Spergularia rubra*; *Spergula pentandra*, *arvensis*, *vernalis*, *salina*, *marginata*; *Malachium aquaticum*, *Holostium umbellatum*, *Cerastium arvense*, *Moenchia erecta*; *Sagina* Linnaei, *decandra* and var. *micrantha*, *apetala* (all *p* or sometimes *t*); *Illecebrum verticillatum* (*h*).

Oxalidaceae: *Oxalis stricta*, *corniculata*, *Lasiandra*, *incarnata*, *lobata*, *Deppii* (all *p* or sometimes *t*).

Cruciferae: *Subularia aquatica* (*h*).

Droseraceae: *Drosera rotundifolia*, *intermedia* (*p* or sometimes *t*).

Compositae: *Taraxicum officinale* (*p* or sometimes *t*).

Scrophulariaceae: *Veronica hederifolia*, *serpyllifolia*, *agrestis*, *triphyllos* (*p* or sometimes *t*).

Primulaceae: *Hottonia inflata* (*h*).

Acanthaceae: *Dicliptera assurgens* (*t*).

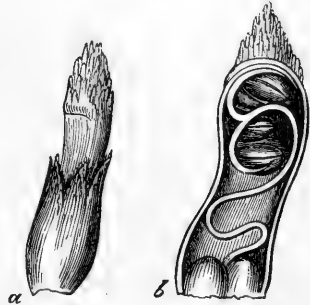


FIG. 8. Cleistogamous Autumn Flower of *Lamium amplexicaule* L. (after Hildebrand): a. external view; b. cut through longitudinally.

Gentianaceae: *Menyanthes* sp. (*h*).

Scleranthaceae: *Scleranthus annuus* (*p* or sometimes *t*).

Alismaceae: *Alisma natans* (*h*).

Butomaceae: *Hydrocleys nymphoides* (*h* or sometimes *p*).

Juncaceae: *Juncus bufonius* and *effusus* (*p* or sometimes *t*).

Glumaceae: *Triticum Spelta*, species of *Stipa*, *Hordeum distichum*, &c. (*t*).

The following pseudo-cleistogamous species should be added to those in Hansgirg's list. Most of them remain closed in dull or rainy weather:—

Papaveraceae: *Hypecoum pendulum* L. (Kerner).

Cruciferae: *Arabis coerulea* *Haenke* (Kerner), *Nasturtium officinale* R. Br. (Knuth).

Caryophyllaceae: *Cerastium semidecandrum* L. (H. Müller), *C. tetrandrum* Curt. (Knuth), *Sagina nodosa* Fz. (Warming), *S. procumbens* L. (Schulz, Warming).

Hypericaceae: *Hypericum humifusum* L. (Kerner).

Geraniaceae: *Erodium maritimum* L'Her. var. *apetalum* (Ludwig).

Scleranthaceae: *Scleranthus annuus* L. (under the snow in winter, Schulz).

Portulacaceae: *Portulaca oleracea* L. (Kerner), *Montia minor* Gmel. (Kirchner).

Rubiaceae: *Galium uliginosum* L. (Schulz).

Compositae: *Filago minima* (Errera and Gevaert).

Campanulaceae: *Campanula uniflora* L. (Warming).

Gentianaceae: *Gentiana prostrata* Kz. and *G. tenella* Rottb.=*G. glacialis* Vill. (Kerner), *G. campestris* L. (Kerner), *Cicendia filiformis* (Errera and Gevaert).

Scrophulariaceae: *Veronica peregrina* L., *V. arvensis* and *V. persica* Poir.=*V. Buxbaumii* Ten. (Kirchner), *Limosella aquatica* L. (hydro-cleistogamous, Kerner).

Primulaceae: *Centunculus minimus* L. (Ascherson).

Polygonaceae: *Polygonum Hydropiper* L. (Kerner), *P. minus* Huds. and *P. mite* L. (Kerner).

Thymelaeaceae: *Passerina annua* L.=*Stellera Passerina* L. (Kerner).

Iridaceae: *Sisyrinchium anceps* Lam. (Kerner).

Liliaceae: *Gagea lutea* (Kerner).

Gramineae: *Avena sativa* L. (Hildebrand), *Bromus secalinus* L. (Hildebrand), *Hordeum distichum* L. (Delpino), *H. Zeocrithron* (Hansgirg), *Secale cereale* L. (ditto).

A few more cases have still to be mentioned in which cleistogamy is induced by prolonged drought, and in which it disappears again on placing the plants in a moister situation. Baron E. Eggers (Bot. Centralbl., Cassel, viii, 1881, pp. 57-9) places in this category the following St. Croix species: *Sinapis arvensis* L.; Acanthaceae,—*Stenandrium rupestre* Ns., *Dicliptera assurgens* Gris., *Stemonacanthus coccineus* Ns., *Dianthera sessilis* Gris. and *Blechum Brownei* Juss.; Rubiaceae,—*Erithalis fruticosa* L.; and the orchid *Polystachya luteola* Hook.

Errera and Gevaert (Bull. Soc. roy. bot., Gand, xvii, 1878) observed the opposite of this in *Subularia aquatica*, which was cleistogamous in a marshy situation, but became chasmogamous when placed in a dry locality.

According to Henslow ('On the Self-fertilization of Plants,' Trans. Linn. Soc. (Bot.), series 2, i, 1877, pp. 317-48) cleistogamy is induced by lack of warmth in

Tradescantia erecta, *Stellaria media*, *Spergula arvensis*, *Cerastium glomeratum*, *Gaura parvifolia*, *Paronychia bonariensis*, *Corrigiola littoralis*, *Scleranthus annuus*, *Herniaria glabra*, *Malva rotundifolia*, and others; according to Mehan (Bull. Torrey Bot. Cl., New York, x, 1883) in *Nemophila maculata Benth.*, *Opuntia leptocaulis DC.*; according to Coulter (Bot. Gaz., Chicago, viii, 1883) in *Cyclamen europaeum*; according to Bush (op. cit., vii, 1882) in *Malvastrum angustum*; and according to Battandier (Bul. soc. bot., Paris, xxx, 1883) in *Portulaca oleracea L.*, and others.

These various forms of pseudo-cleistogamy point to the causes of genuine cleistogamy: deficiency of light, air, warmth, dryness, or moisture are to be regarded as such. Darwin referred the origin of cleistogamous flowers to developmental retardation of chasmogamous forms, due partly to deficiency, but also partly to an excess of light, and perhaps also to lack of insects (cf. my note on p. 54).

Observation actually proves that even genuine cleistogamy may be produced by deficiency of light. Kerner ('Nat. Hist. Pl.,' Eng. Ed. 1, II, p. 395), for instance, noticed that *Viola sepincola* does not form any open flowers in the deep shades of woods, but does form them in open country in situations that from time to time receive sunlight. The investigations of Vöchting (Jahrb. wiss. Bot., Leipzig, xxv, 1893) agree with this, as he proved experimentally that with feeble illumination there is frequent degeneration of the conspicuous parts, and formation of cleistogamous flowers. And he also is of opinion that defective illumination is of primary importance in the evolution of cleistogamy.

The question whether there are plants which bear cleistogamous flowers only was at first answered in the affirmative. A. Batalin (Bot. Ztg., xxix, 1871, pp. 388-92) maintained that *Juncus bufonius* is regularly self-fertilized, its flowers always remaining closed. It was, however, established by Ascherson (op. cit., 1871, pp. 551-5; 1872, pp. 697-9, 738, 739), Buchenau (op. cit., 1871, pp. 845-52), and Haussknecht (op. cit., pp. 802-7) that while numerous flowers fade with enclosed pistil and anthers, others on the contrary open out to 180° in a stellate way, so that they may also be fertilized by foreign pollen; and it was also shown that between these two kinds of flower there are numerous intermediate forms (cf. F. Buchenau, 'Bestäubungsverhältnisse der Juncaceen,' Jahrb. wiss. Bot., Leipzig, xxiv, 1892, pp. 363, 364, 382).

There is also an African species of *Salvia* which was at one time supposed to bear cleistogamous flowers only. It was therefore named *S. cleistogama de Bary et Paul*, and was regarded by Ascherson (Bot. Ztg., xxix, 1871) as an example of a plant propagating continuously by self-fertilization. As a matter of fact, the plant bore cleistogamous flowers only during the first five years of its cultivation at Halle, but afterwards chasmogamous flowers appeared as well.

Recently (1883) some cases of the constant occurrence of completely closed, but otherwise normally formed flowers have been announced by W. Burck (Ann. Jard. bot., Buitenzorg, iv, pp. 17-20). In *Myrmecodia echinata Gaud.*, e.g., the flowers are completely closed by fusion of the four corolla-lobes, although there are secreting nectaries developed beneath a ring of hairs. The stigmas, which are papillose on the outer side, alternate with the anthers, and by growth of the corolla the pollen of these anthers is brought into contact with the stigmatic

papillae. So that flowers originally adapted to the visits of insects are now modified by the closing of the ingress, only self-fertilization takes place, and chasmogamous forms are wanting (?).

Burck (op. cit., viii, 1890, pp. 122-62) has subsequently discovered other similar cases of perfectly closed, but otherwise normally formed flowers in Anonaceae; as, for example, *Unona coelophlæa* Scheff., and others, *Artabotrys suaveolens*, *A. Blumei*, *Goniiothalamus giganteus* Hook. et Th., and *Cyathocalyx zeylanica*. From their occurrence he draws the inference that Nature has altered her original plan of cross-fertilization, owing to subsequent modifications in the conditions of life of the species in question, and has gradually adapted them to self-fertilization exclusively. The closing of the flowers is possibly to be explained as an adaptation for protection against ants (according to Loew, 'Einführung in die Blütenbiologie,' p. 311, note).

According to Koehne, *Ammannia latifolia* is also exclusively cleistogamous. For such flowers the term *archo-cleistogamous* might be introduced.

Many cleistogamous flowers bend their stalks in such a way that the fruits which develop are buried in the earth. Excellent protection is thus afforded to the seeds, but their dispersal is seriously prejudiced. Such phenomena are known in species belonging to the genera *Amphicarpæa*, *Commelina*, *Linaria*, *Oxalis*, *Vandellia*, *Vicia*, *Viola*, *Voandzeia*, and also in *Cardamine chenopodifolia* Pers. (Grisebach).

The culture experiments made by H. Hoffmann ('Kulturversuche über Variation,' Bot. Ztg., xli, 1883) with cleistogamous flowers gave as a result for *Lamium amplexicaule* that the offspring were only partly cleistogamous, and this was specially the case after close sowing. In *Hordeum vulgare* L. var. *nudum*, almost all the flowers that were raised throughout a decade were cleistogamous.

Besides those already named, the following plants have from time to time been recognized as examples of true cleistogamy:—

Cruciferae: *Subularia aquatica* (Hiltner), *Thlaspi arvense* (Hieronymus).

Malpighiaceae: *Camarea* St. Hil. and *Janusia* A. Juss. (Jussieu), *Aspicarpa urens* Rich. (H. v. Mohl), *Gaudichaudia* H. B. K. (Kuhn).

Violaceae: *Viola mirabilis* (Dillenius, 1732; Linnaeus, 1749), *V. nana* (Darwin), *V. Roxburghiana* (Darwin), *V. stagnina* (H. Müller), *V. sylvatica* (Corry and Bennett), *V. arenaria* (Kerner), *V. canina* (Kerner), *V. hirta* var. *Salvatoriana* n. f. (Calloni), *V. sepincola* Kerner (Kerner), *V. sciaphila* (Calloni), *V. elatior* (H. v. Mohl), *V. biflora*, *V. of the Campos of St. Catharina* (Fr. Müller), *V. cucullata*, *floribunda*, and *sagittata* (Bennett), *V. sarmentosa* Dougl. (Meehan), *V. suberosa* (Battandier), *V. filicaulis* and *Cunninghamii* (G. M. Thompson).

Cistaceae: *Helianthemum guttatum* (Linnaeus, Ascherson), *H. kahiricum* Del., *Lippii* Pers. var. *micranthum* Boiss. (ditto).

Droseraceae: *Drosera anglica* (Darwin), *D. rotundifolia* (Knuth), *D. intermedia* (Knuth), *Aldrovandia vesiculosa* (Bentham and Hooker, Korczinski).

Polygalaceae: Species of *Polygala* (Darwin).

Silenaceae: *Silene vilipensa* Knze., *hirsuta* Lag., *gallica* L., *cerastoides* L., *tridentata* Desf., *clandestina* Jacq., *longicaulis* Pourr., *apetala* W., *inaperta* L., *antirrhina* L. (all by Batalin).

Alsineaceae: *Cerastium viscosum* *L.* (Batalin), *C. glomeratum* (Warming).

Malvaceae: *Pavonia hastata* *Cav.* (Heckel).

Rosaceae: *Dalibarda repens* (Pringle and Asa Gray).

Balsaminaceae: *Impatiens Noli-tangere* (H. v. Mohl), *I. fulva* *Nutt.*, &c. (Loche).

Oxalidaceae: *Oxalis Acetosella* *L.* (H. v. Mohl), *O. sensitiva* (Darwin).

Papilionaceae: *Vicia amphicarpa* (Kuhn, H. v. Mohl, Kiefer), *Trifolium polymorphum* (Darwin) and other sp. (Kuhn), sp. of *Parochaetus Ham.*, *Stylosanthes Swartz*, *Heterocarpaea Phil.*, *Lespedeza Rich.*, *Chapmannia Torr. et Gray*, *Arachis*, *Lathyrus* (all by Kuhn), *L. setifolius* (Kiefer), *Amphicarpea* (Torrey, Asa Gray), *Neurocarpum Desv.*, *Martinsia Schult.*, *Glycine L.*, *Galactia*, *Voandzeia Pet. Thouars* (all by H. v. Mohl, Kuhn), *Ononis columnae* (Darwin), *O. parviflora* (ditto), *Tephrosia heteranthera* (Hieronymus).

Onagraceae: *Oenothera tenella Bert.* = *Godetia Cavanillesii Spach* (Philippi).

Lythraceae: *Ammannia latifolia* and *verticillata* (Koehne), *Peplis*, *Lythrum nummulariaefolium* and *thesoides* (ditto), *Rotala*, *Nesaea* (ditto).

Portulacaceae: *Portulaca grandiflora Lindl.* (De Bonis).

Paronychiaceae: *Polycarpon tetraphyllum* (Batalin).

Scleranthaceae: *Scleranthus annuus L.* (Schulz).

Campanulaceae: *Campanula canescens Wall.* and *C. colorata Wall.* (H. v. Mohl), *C. dimorphantha Schweinf.* (Ascherson), *Specularia perfoliata Dl.* (Linnaeus, H. v. Mohl).

Oleaceae: Sp. of *Jasminum* (Kuhn), sp. of *Forsythia* (Darwin).

Asclepiadaceae: *Hoya carnosa* (Darwin), *Stapelia* (Kuhn).

Polemoniaceae: *Collomia grandiflora Lindl.* (Ludwig, Scharlok).

Convolvulaceae: *Cuscuta* (Kuhn), *C. Epithymum* (Knuth), *Ipomoea pes tigridis* (Kuhn).

Boraginaceae: *Lithospermum longiflorum Pursh* (Darwin), *Eritrichium* (Kuhn).

Acanthaceae: *Cryphiacanthus barbadensis Nees* = *Ruellia clandestina L.* (Dillenius), *Eranthemum L.*, *Daedalacanthus Anders.*, *Dipteracanthus Nees*, *Aechmanthera Nees*, *Ruellia L.* (Darwin).

Scrophulariaceae: *Vandellia pyxidaria Maxim.* = *Lindernia pyxidaria All.* (Maximowicz, Urban), *V. sessiflora Benth.* (Kuhn), *V. nummularifolia* (Darwin), *Veronica*, *Buxbaumii*, *polita*, and others (Darwin), *Linaria* (Michalet, Kuhn), *Scrophularia* (Kuhn), *S. arguta* (Trelease), *Salpiglossis sinuata R. et Pav.* (De Bonis).

Labiatae: *Salvia lanigera Poir.* (Ascherson), *Lamium amplexicaule* (Hildebrand, Kerner, Hoffmann, Kiefer), *Ajuga Iva* (Ascherson).

Primulaceae: *Hottonia palustris* (Darwin), *Androsace Vitaliana K. S.* (Treviranus), *Dionysia* (Kuhn).

Plantaginaceae: *Plantago* (Kuhn), *Anandria* (Kuhn). *Plantago virginica*, cultivated (Ludwig).

Polygonaceae: *Polygonum Persicaria*, *aviculare*, *Hydropiper*, and many other sp. (Meehan).

Nyctaginaceae: *Oxybaphus* (Darwin), *Nyctaginia* (ditto).

Thymelaeaceae: *Leucosmia* (Darwin, Hildebrand).

Orchidaceae: *Schomburgkia*, *Cattleya*, *Epidendron*, and others (Kuhn).

Pontederiaceae: *Heteranthera* (not *Monochoria*) *Kotschyana Fzl.*, *H. reniformis*, *H. spicata*, *H. callaefolia*, *H. Potamogeton*, and other sp. (Solms-Laubach).

Commelinaceae: *Commelina bengalensis* (Weinmann), *Tradescantia erecta* (Henslow).

Juncaceae: *Juncus* (Darwin), *J. capitatus* (Buchenau), *J. pygmaeus* (? , Buchenau).

Gramineae: *Hordeum* (Darwin), *H. vulgare* (a few flowers, Delpino), *Cryptostachys* (Darwin), sp. of *Stipa* (Godron), *St. pennata* (Hackel), sp. of *Bromus* (Beijerinck), *Leersia oryzoides* (Duval-Jouve, Ascherson, Kiefer), *Amphicarpum*, *Danthonia spicata* and related sp. (Pringle and Asa Gray), *Vilfa* (Pringle), *Diplachne serotina* (Janka and Hackel), *Vulpia Myuros*, *sciuroides*, and *ciliata* (Kiefer).

Connected with cleistogamy is the so-called bud-fertilization, cases of which have been more particularly observed in orchids, e. g. in *Limodorum abortivum* (Freyhold), *Thelymitra carnea* and *longifolia* (Fitzgerald), *Polystachya luteola* (E. Eggers), *Polystachya zeylanica*, *Phajus villosus*, and *Calanthe inaperta* (Moore), *Maxillaria rufescens* (Reichenbach fil.).

VII. Parthenogenesis.

A few remarks may here be introduced concerning Parthenogenesis (virgin reproduction) of flowering plants. The term signifies *the formation of germinable seed without the aid of pollen*. It is well known that the first observation on this phenomenon was published by J. Smith (Trans. Linn. Soc., xxi, 1841, p. 509): A female plant of the dioecious species *Caelebogyne ilicifolia*, grown in the Botanic Gardens at Kew, from 1829, produced seed capable of germinating, necessarily without previous fertilization. A. Braun, by examining a cultivated plant in the Botanic Gardens at Berlin, established the correctness of Smith's observation and compared the phenomenon with the parthenogenesis of insects discovered by Th. v. Siebold (1856). Deecke, indeed, observed individual pollen-tubes, while Baillon and Karsten saw isolated anthers in the otherwise purely female flowers, but A. Braun's further observations ('Über Polyembryonie und Keimung bei *Caelebogyne*,' Berlin, 1860) contradicted those of the botanists named. It was only in 1878 that Strasburger ('Über Polyembryonie,' *Jenaische Zs. Natw.*, xii, 1878) cleared up the matter by proving that this case finds an analogue in the occurrence of so-called adventitious embryos, e.g. in *Funkia ovata*, *Allium fragrans*, *Euonymus latifolius*, sp. of *Citrus*, and others, in which individual nucellar cells in the neighbourhood of the embryo-sac, grow into this as rounded bodies, that multiply by cell-division and develop into adventitious embryos without the direct influence of fertilization. In *Caelebogyne* the proliferating nucellar cells, which are growing into adventitious embryos, press upon the disorganized egg-apparatus. This case, therefore, differs from the other only in the complete suppression of fertilization, but is in complete agreement with it, so far as concerns the development of adventitious embryos independently of fertilization. And this proves that the embryo-production in *Caelebogyne* is not really parthenogenetic, though further development takes place of an egg-nucleus that remains unfertilized. It represents, on the contrary, a process of asexual reproduction, similar to the apogamy of many ferns, or the vivipary in spikelets of grasses (Loew, 'Einführung in die Blütenbiologie,' p. 296).

Kerner has recently again called the attention of botanists to Parthenogenesis, by seeking to prove that it appears beyond doubt in *Mercurialis annua*. On account of the great importance of this subject, I give Kerner's description ('Nat. Hist. Pl.,' Eng. Ed. 1, II, pp. 465, 466) verbatim:—'At various times,' he says, 'female plants have been reared quite alone in pots, and it has appeared that these have developed seeds which, though fewer in number, are just as capable of germination as those produced by plants growing in the open country in the company of male stocks. This result was doubted on all sides, and efforts were made to show that it was due to the uncertainty of culture experiments. It was maintained that pollen-dust might be carried from afar by the wind into the rooms made use of for the experiments, and what seemed even more important, attention was called to the fact that some plants with many female flowers may also bear a few male flowers. These criticisms stimulated new experiments, in which suitable care was taken to avoid all possible sources of error. For the new experiments those districts appeared specially favourable where for many miles round no dog's mercury was to be found growing wild, and where therefore the possibility of the introduction of pollen from the surrounding district was altogether excluded, as for instance some point in the middle Tyrol, where both the annual and the perennial dog's mercury are altogether absent. In such a district in the high-lying Tyrolean Gschnitzthal, I repeated the experiments that had been made in 1833 by Ramisch, in Prague, with so much perseverance, and, in my work, all those errors which had been attributed to the experiments of Ramisch, were avoided. In particular, all plants on which buds of male flowers appeared were at once destroyed, and careful attention was given to ascertain whether some individual male or hermaphrodite flower might not possibly be concealed on one or other of the female plants. At the time when the stigmas of the dog's mercury were ready for pollination there were quite certainly for miles round no wild pollen-cells of the plant, and fertilization by such pollen was therefore out of the question. But, notwithstanding this, the carpels soon became swollen, embryo-containing seeds developed from the ovules, and when these seeds were sown vigorous young plants of dog's mercury grew up.'

Perhaps *Antennaria alpina* Gaertner (*Gnaphalium alpinum* L.) is also parthenogenetic in the arctic regions, since, according to Vahl, Lange, and Warming, male flowers of this dioecious plant are there unknown, although it fruits in numerous localities. On the other hand, Hartman (Handbok i Skand. Flora, p. 7) describes male plants from specimens which were found in 1847 by Laestadius (Loew, 'Blütenbiol. Floristik,' p. 111).

Kerner ('Nat. Hist. Pl.,' Eng. Ed. 1, II, p. 465), incited to observation by these facts, has cultivated to the flowering-stage plants of *Gnaphalium alpinum* from the Dovrefjeld in Norway, using every possible precautionary measure. All the flowers developed ovules, but no pollen, so that pollination of the stigmas was quite impossible. Yet some of the ovules became fruits with well-formed seeds, which germinated into young plants when sown in sandy humus. These young plants agreed in every respect with the parent stock and soon flowered, but, as before, their flowers only bore carpels. From these results Kerner concludes that there can be no doubt that *G. alpinum* multiplies by parthenogenesis in its remote northern habitat, and that reproduction is not prevented by the failure of pollen-producing plants.

Other known cases of parthenogenesis occur among orchids, grasses, and *Hippeastrum*; on the other hand, according to Bonavia (Gard. Chron., London, viii, 1890), the development of embryos of *Ficus Roxburghii* without pollen, as observed by Cunningham (loc. cit.) has not been sufficiently proved.

A. Ernst ('A new case of Parthenogenesis in the vegetable kingdom') found that in *Disciphania Ernstii* *Eickl.* (in Caracas) two plants produced an increasing number of fruits in three successive years, although the nearest male plants were nine miles away from the place of observation, so that there could be no question of cross-fertilization¹.

VIII. Flower-Groups.

As already mentioned on p. 14, Delpino, in his work 'Ulteriori osservazioni sulla dicogamia nel regno vegetale,' has arranged the floral mechanisms known to him in adaptational groups, and so has established a classification of plants according to their mode of fertilization. His scheme, which embraces the whole vegetable kingdom, is as follows:—

A. ZOOGAMAE: plants with reproductive elements capable of movement. Among these are most of the Cryptogams, in which the spermatozoids are motile.

B. DIAMESOGAMAE: plants in which the reproductive elements require external means of conveyance.

I. **Hydrophilae** (*Water-pollinated Plants*): plants which are pollinated by the agency of water.

(a) Pollination is effected *under* water: the pollen-grains or the spores possess the specific gravity of water: *Posidonia*, *Cymodocea*, *Zostera*, *Ceratophyllum*, *Florideae*.

(b) Pollination is effected *on the surface* of the water: the pollen is lighter than water, or is borne on a float; the stalks of the female flowers grow up to the surface of the water: *Ruppia*, *Vallisneria*.

II. **Anemophilae** (*Wind-pollinated Plants*): plants which are pollinated by the agency of wind.

(a) Wind-pollinated plants *without* stigma: *Gymnosperms*.

(b) Wind-pollinated plants *with* stigma—this being usually well developed.

1. *Catkin form* (*typus amentiflorus*): the male inflorescences have long movable axes (*Corylus*, *Betula*, and so forth).

2. *Form with pendulous flowers* (*typus penduliflorus*): *Negundo* *fraxinifolium*, *Rumex*.

3. *Form with long movable filaments* (*typus longistamineus*). This very common form of wind-pollinated flower occurs in almost all *Gramineae*, *Cyperaceae*, and *Juncaceae*, also in *Cannabis*, *Humulus*, *Mercurialis*, *Ricinus*, *Plantago*, *Litorea*, sp. of *Callitriche*, *Myriophyllum*, *Hippuris*, and others.

4. *Form with elastic explosive stamens* (*typus explodens*): *Urtica*, *Parietaria*.

¹ [Other cases have been recorded since the publication in 1898 of the German text. A useful summary with references to the literature will be found in Coulter and Chamberlain, 'Morphology of Angiosperms,' New York, 1903.—ED.]

5. *Form with immobile flowers (typus immotiflorus)*: Sparganium, Typha, Potamogeton, Triglochin, many Palms.

III. **Zoidiophilae** (*Animal-pollinated Plants*): after correspondence with Hermann Müller, Delpino proposed to divide this group of floral arrangements as follows (according to Herm. Müller, 'Fertilisation,' pp. 15-16):—

(a) *Ornithophilae* (*Bird-pollinated Plants*): plants with flowers pollinated by the agency of honey-sucking birds, or those that capture small insects (Trochilus, Nectarinia, and others). Many of these flowers are exceedingly large and saccular. They are characterized by their vertical position and brilliant (especially scarlet) colours, and they often secrete large quantities of nectar.

(b) *Malacophilae* (*Snail-pollinated and Slug-pollinated Plants*): plants with flowers pollinated by the agency of snails or slugs. The flowers are so closely crowded that in gliding over them these creatures must come into contact with pollen and stigmas. Some of these are protected against the injurious effects of their voracious visitors by secreting an irritant fluid that is fatal to snails and slugs (*Alocasia odora*), or by conversion of their perianth into a fleshy, edible tissue, with the consumption of which the visitors are satisfied (*Rhodea japonica*).

(c) *Entomophilae* (*Insect-pollinated Plants*): plants with flowers pollinated by the agency of insects. To this group belong all the plants indigenous to Europe that are popularly known as 'flowers,' i.e. flowers that are immediately conspicuous to us, and to their visitors, through their bright colour, pleasant odour, or both (Herm. Müller, 'Fertilisation,' p. 16, note). Delpino distinguishes the following special sub-groups:—

1. *Melittophilae* (*with Large-Bee Flowers*): plants with flowers pollinated by the agency of large bees. These are day-flowers, of which the colours and odours are also agreeable to man; some of them possess concealed nectar (*Salvia pratensis*). Others are devoid of nectar, and these possess hidden pollen, which only appears after special treatment (*Genista tinctoria**)¹.

2. *Micromelittophilae* (*with Small-Bee Flowers*): plants with flowers pollinated by small bees (and a great variety of other small insects). They influence the visitors to a much higher degree than in the case of any other plants (*Herminium Monorchis*?).

3. *Myiophilae* (*with Fly Flowers*): plants with flowers pollinated by Dipterids of all kinds. The flowers are mostly dull in colour (yellowish, claret, spotted), and usually have a smell that is disagreeable both to men and to bees. The nectar is quite exposed, or there is pollen only (*Euonymus*).

4. *Micromyiophilae* (*with Small-Fly Flowers*): plants with flowers pollinated by tiny Dipterids. The flower or the inflorescence forms a closed chamber with narrow entrance, and this serves often as a temporary prison for the visitors. There is an extremely thin layer of nectar, or none at all, but in the latter case there is abundant pollen (*Aristolochia Clematitis*, *Arum*).

5. *Sapromyiophilae* (*with Carrion-Fly Flowers*): plants with flowers pollinated

¹ Forms indicated by * have been added by Hermann Müller, from his own lists, to Delpino's groups.

by carrion- or dung-flies, also by beetles. They are characterized by the smell of carrion, and otherwise are like 3. (*Stapelia*, *Rafflesia*).

6. *Cantharophilae* (*with Beetle Flowers*): plants with flowers pollinated by beetles. These are large day-flowers with conspicuous colours. They afford a convenient shelter, and a superabundance of pollen, and in many cases there is nectar that is moderately exposed (*Magnolia*).

7. *Psychophilae* (*with Butterfly Flowers*): plants with flowers pollinated by butterflies. Day-flowers of bright colour, with nectar hidden at the base of a very narrow tube (*Dianthus**).

8. *Sphingophilae* (*with Sphinx Flowers*): plants with flowers pollinated by Hawk-moths and Noctuids. Night-flowers of pale colour and strong agreeable odour, with nectar hidden at the bottom of a very long corolla-tube, or in a spur (*Lonicera Caprifolium**, *Platanthera**).

Delpino subsequently published the preceding classification of insect-pollinated plants in 'Ult. oss.' (*Atti. Soc. ital. sc. nat.*, Milano, xvi, 1874), p. 152. It has the defect that all plants are left out of account which are visited and pollinated by insects of various orders indiscriminately, i.e. the large majority of 'flowers.' Herm. Müller accordingly proposed the following classification of flowers ('*Alpenblumen*,' pp. 477-511)¹.

1. *Pollen-flowers*, which he indicated by the symbol **Po**: they offer no nectar to visitors, but only pollen, e.g. species of the genus *Papaver*.

2. *Flowers with exposed nectar* (symbol **A**). The nectar lying quite exposed is at once seen, and is consequently accessible to all kinds of insects. To this group belong most of the *Umbelliferae*, e.g. *Daucus Carota*.

3. *Flowers with nectar partly concealed* (**AB**). The honey is only visible in favourable circumstances, and in bright sunshine. Almost all *Cruciferae* belong to this group, e.g. *Raphanus Raphanistrum*.

4. *Flowers with completely concealed nectar* (**B**). The nectar is covered by projecting parts of the flower, hairs, points, &c., or is concealed in sacs, so that it is quite out of sight of visitors. *Thymus Serpyllum*.

5. *Social Flowers* (**B'**). The nectar is concealed as in the previous class, but the flowers are united into heads. To this group belong all the *Compositae*, e.g. *Centaurea Cyanus*.

6. *Hymenopterid Flowers* (**H**). These can only be pollinated and plundered by Hymenopterids. To this group belong all the papilionaceous flowers, e.g. *Genista pilosa*.

7. *Lepidopterid Flowers* (**F**). These are chiefly visited by butterflies, the long thin proboscis being able to reach the nectar, which is hidden in deep narrow tubes or spurs. *Dianthus Carthusianorum*, *Lonicera Periclymenum*.

8. *Dipterid or Fly Flowers* (**D**). These are visited chiefly by flies. *Ruta graveolens*, *Parnassia palustris*, *Aristolochia Clematitis*, *Vincetoxicum officinale*, *Veronica Chamaedrys*.

9. *Small-insect Flowers* (**Kl**). These are visited by quite small insects of very different orders. *Herminium Monorchis*.

¹ [The symbols of Müller and Verhoeff are here given, but several of them are replaced by others in the body of the translation. See p. 67, footnote.—Tr.]

As I have pointed out in my 'Grundriss der Blütenbiologie' (p. 9, note), Herm. Müller's nine classes of flowers may readily be extended to twelve, inasmuch as social flowers with exposed nectar may be distinguished from those with partially concealed nectar. For these two groups the symbols **A'** and **AB'** would be appropriate. The compound umbels of the Umbelliferae (especially of those with radiating marginal flowers), and the cymes (especially again those with neuter enlarged marginal flowers, e.g. those of *Viburnum Opulus*) also form an oecological unity, comparable with, e.g., the capitula of the Compositae, for like these they serve as a whole to entice insects, and also secure simultaneous pollination of numerous flowers by the passage of insects over the one continuous surface formed by the inflorescence. As examples of the class **AB'**, the corymbs of some Cruciferae may be taken, especially those of *Iberis* and *Teesdalia*, because in these the flowers at the margin of the inflorescence are larger than those in the middle. Accordingly, the following classes of flowers would result:—W (i.e. wind-pollinated or anemophilous flowers), Po, A, A', AB, AB', B, B', H, F, D, Kl.

C. Verhoeff, in his work 'Blumen und Insekten auf der Insel Norderney' (Nova Acta Leop., Halle, lxi, 1894, pp. 174 and 175), attempts to change the classification of Herm. Müller in accordance with the comparatively few plants investigated by him with regard to their flower pollination on the island of Norderney¹. He distinguishes:—

1. *Wind-pollinated Flowers* (W): no adaptation to insects, but occasionally visited by them. *Hippophaë rhamnoides*.

2. *Actinomorphic Pollen-flowers* (Po A): pollen adhesive, corolla usually coloured, no nectar. *Cochlearia anglica*, *Helianthemum*, *Rosa*, *Polygonum aviculare*.

3. *Zygomorphic Pollen-flowers* (Po B): general character as before. *Sarothamnus scoparius*.

4. *Nectar Flowers* (Ne): no coloured perianth-leaves or petals, producing nectar, sticky pollen. *Salix*.

5. *Flowers with exposed nectar, but not social* (A): brightly coloured perianth leaves or petals, nectar exposed, pollen sticky. Actinomorphic. *Ranunculus Flammula*, *Batrachium*, *Honckenya*, *Parnassia*.

6. *Flowers adapted in the same way but associated in crowded small-flowered societies* (AG). Most of the Rubiaceae and Umbelliferae.

7. *Flowers with partly concealed nectar*; quite or almost actinomorphic (AB): *Ranunculus acris*, *repens*, *sceleratus*; Cardamine, *Stenophragma*, Brassica, *Capsella*, *Sisymbrium*, *Cerastium*, *Rubus*, *Sedum*, *Glaux*, *Polygonum Persicaria*.

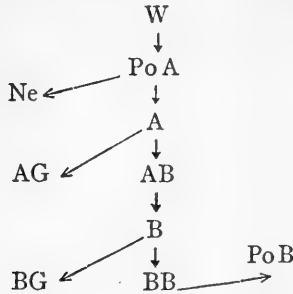
8. *Flowers with completely concealed nectar*; sometimes actinomorphic, sometimes zygomorphic (B): pollen not concealed. *Silene*, *Lychnis*, *Erodium*, *Epilobium*, *Vaccinium*, *Calluna*, *Pyrola* (a specially adapted form, according to Verhoeff), *Myosotis*, *Veronica*, *Euphrasia*, *Mentha*, *Stachys*, *Armeria*, *Orchis*, *Asparagus*.

9. *Flowers with nectar equally well concealed, but the flowers united into capitulate societies* (BG): pollen not concealed. Most Compositae, and *Jasione*—the latter with nectar not quite so deeply hidden.

¹ See note on preceding page.

10. *Flowers with adaptation B, but in which the pollen also is more or less completely concealed (BB).* Zygomorphous. *Viola*, *Anthyllis*, *Trifolium*, *Lotus*, *Vicia*, *Linaria*, *Alectorolophus*.

Verhoeff represents the most important relationships between his ten chief stages of adaptation in the following scheme:—



The classification presents no advance upon that of Müller, for the Zygomorphous Pollen-flowers (*Sarothamnus*, *Genista*, *Ulex*) are such well-marked Hymenopterid Flowers, that they cannot possibly be separated from the Nectar-flowers of this group (*Anthyllis*, *Trifolium*, *Lotus*, *Vicia*, &c.). Such separation would be like the artificial division of the Papilionaceae into two separate classes (XVI and XVII) in the Linnean classification, according as they are monadelphous or diadelphous. And it may be added that the term 'nectar-flowers' is applicable not only to the extremely simple nectar-containing flowers of *Salix*, but also to Verhoeff's classes A, AG, AB, B, BG, BB.

Loew (*Beob. über den Blumenbesuch von Insekten . . . Weit. Beob. über den Blumenbesuch . . .*, *Beitr. zur blütenbiolog. Statistik*) has arranged the floral classes of Hermann Müller (excluding, however, classes **D** and **K1**) in the following three groups:—

I. Allotropic Flowers: these are adapted to various kinds of insects possessing a *short* proboscis. To this group belong classes **W**, **Po**, **A**, and **AB**.

II. Hemitropous Flowers: these are imperfectly adapted to some definite set of insects possessing a proboscis of *medium* length. To this group belong classes **B** and **B'**.

III. Eutropous Flowers: these are more or less exclusively adapted to a definite set of insects possessing a *long* proboscis. To this group belong Bee Flowers, Humble-bee Flowers, and Lepidopterid Flowers.

Loew distinguishes three groups of insects, the visitors, respectively, of allotropic, hemitropous, and eutropous flowers. These will be discussed later.

Taking into account the observations first made (1892) by W. Burck, and confirmed (1897) by J. H. Hart, which prove that bats act as pollinating-agents, and collating the groupings of Delpino and Müller, the following classification of plants, according to their flower pollination, may be advanced¹:—

¹ Kerner ('*Die Schutzmittel des Pollens*,' pp. 45, 46, note) employs the term *Kangaroo flowers* in describing the floral arrangements of *Dryandra* (Proteaceae). The flowers are inserted on the rim

I. Water-pollinated plants, *Hydrophilae*, Hy (Delpino).

- (a) *Pollinated under water, Hyphrogamicæ* (Knuth).
- (b) *Pollinated on the surface, Ephrogamicæ* (Knuth).

II. Wind-pollinated plants, *Anemophilæ*, An (Delpino).

- (a) *Stigma absent, Astigmaticæ* (Knuth).
- (b) *Stigma present, Stigmaticæ* (Knuth), with—
 1. Flowers in catkins, *Amentifloræ* (Delpino).
 2. Pendulous flowers, *Pendulifloræ* (Delpino).
 3. Long filaments, *Longistaminæ* (Delpino).
 4. Explosive flowers, *Explodifloræ* (Delpino).
 5. Immotile flowers, *Immotifloræ* (Delpino).

III. Animal-pollinated plants, *Zoidiophilæ*, Z (Delpino), with—

- (a) *Bat-pollinated flowers, Chiropterophilæ, Ch* (Knuth).
- (b) *Bird-pollinated flowers, Ornithophilæ, O* (Delpino).
- (c) *Snail-pollinated or Slug-pollinated flowers, Malacophilæ, M* (Delpino).
- (d) *Insect-pollinated flowers, Entomophilæ, En* (Delpino).
 - (a) *Pollen flowers, Po* (Müller).
 - (b) *Nectar flowers, Ne*¹ (Knuth).
 1. *Flowers with exposed nectar, E* (Müller).
 2. *Flowers with partly concealed nectar, EC* (Müller).
 3. *Flowers with concealed nectar, C* (Müller).
 4. *Social flowers, S* (Müller).
 5. *Hymenopterid flowers, H* (Müller).
 - (a) Bee flowers, Hb.
 - (b) Humble-bee flowers, Hh.
 - (c) Bee-humble-bee flowers, Hbh.
 - (d) Wasp flowers, Hw.
 - (e) Ichneumon flowers, Hi.
 - 6. *Lepidopterid flowers, L* (Müller).
 - (a) Butterfly flowers, Lb.
 - (b) Moth flowers, Lm.
 - 7. *Fly flowers, F* (Müller).
 - (a) Nauseous flowers, Fn.

of a circular dish-shaped depression, which is filled with nectar smelling like sour cream. Kerner says that the position of the stiff somewhat inwardly curved gynophore, to the tip of which pollen adheres, does not seem to be an adaptation to insects; but a kangaroo, which equals in height the average bushes of *Dryandra*, would when licking the nectar and introducing its snout into the cup-shaped inflorescence, undoubtedly remove pollen from the stamens that surround the cup, and might transfer it to another inflorescence. But until direct observations are forthcoming 'kangaroo flowers' cannot be included in our classification.

[The symbols here given, which will be used throughout this translation, correspond to words employed in English books, and therefore deviate in many cases from Müller's symbols.—TR.]

¹ Certain flowers included here are devoid of nectar, especially some *Papilionaceæ* (*Ulex*, *Sarothamnus*, *Genista*), but they cannot, as explained above, be separated on that account from the other flowers of class H. Other flowers placed here are *False Nectar flowers*, and their sugary juices must first be bored for (e.g. *Orchis*); or they may offer to visitors the contents of little knobs filled with sweet sap.

- (b). Pitfall flowers, Fpf.
 - (c) Pinch-trap flowers, Fpt.
 - (d) Deceptive flowers, Fd.
 - (e) Hover-fly flowers, Fh.
8. *Small-insect flowers*, **Sm** (Müller).

I. WATER-POLLINATED PLANTS, HYDROPHILÆ (**Hy**).

It is comparatively seldom that water serves as the agent for carrying pollen to the stigmas of flowering plants. It is characteristic of the pollen of many plants that bloom in water, that the grains should not possess an outer coat (extine). The specific gravity of the pollen (or of the male flowers) is either about equal to that of water, or it is less. In the former case, pollination is effected under water (*Hyphydrogamy*), in the latter case it takes place at the surface of the water (*Ephydrogamy*). Naias, e.g., belongs to the former group of water-flowers, for its pollen-cells (owing to enclosed starch-grains) are rather heavier than water, so that they sink down and are caught by the female flowers.

The process is somewhat different in the case of *Ceratophyllum*. Long after Vaucher, in his 'Histoire physiologique des plantes d'Europe' (1841), had described the fertilization of species of this genus by pollen swimming about in the water as 'körnige Materie' (granular matter), Ludwig (1881) observed that the stamens are made up of a lower part next the short stalk, consisting of two lateral anther-lobes, and an upper part, the 'Auftrieb' (float), composed of air-containing tissue, and produced into two little spines. This arrangement makes the stamen specifically lighter than the water, and it consequently rises to the surface. During this ascent the anthers dehisce, and the large pollen-grains, which are of the same specific gravity as the surrounding medium, are dispersed through the water in which the plants grow, so that the female flowers are necessarily fertilized.

Pollination of flowers on the surface of the water is a more frequent occurrence. In *Callitriche autumnalis* the pollen is lighter than the water, and therefore rises to the surface, where fertilization results. The same is the case in *Ruppia spiralis*, in which the stalk of the female inflorescence stretches up spirally to the surface of the water, where the female flowers are fertilized by pollen-grains that have also floated up. The relations are similar in *Vallisneria spiralis*, as also in the allied *Enalus acoroides*, native to the Indian Ocean. In these plants the female flowers ascend as before on spirally wound stalks to the surface of the water, while the entire male flowers become liberated from the plant, and also rise to the surface, after which the pollen is discharged, and the female flowers are fertilized by it. After this has been effected, the spirally wound flower-stalk of the female flower coils up again, so that the fruits mature under water. In its native country (America) the male flowers of *Elodea canadensis* also float and pollinate the female flowers that reach up to the surface. Only female plants of this species occur in Europe (since 1836). In *Zostera marina* ('sea-grass'), the two filiform forked stigmas grow out from the flower-sheath in the first stage of flowering, and are pollinated by swimming pollen that has been shed from older inflorescences. In the second stage of flowering all the anthers of the inflorescence dehisce simul-

taneously, the pollen they discharge into the water floats up to the surface. *Zannichellia*, allied to the 'sea-grass' is probably also hydrophilous.

Kerner ('Nat. Hist. Pl.,' Eng. Ed. 1, II, pp. 130-2) has given the following somewhat different account of the process of pollination in some of the above-mentioned plants. Although the surface of the water is very near, the pollen of *Vallisneria spiralis*, which consists of sticky clumps, is not easily wetted, for the three petals that are underneath serve as boats, which are swayed by the gentler oscillations of the water without capsizing. These little skiffs are driven here and there by the wind, and in the neighbourhood of any fixed body. If the bays of a *Vallisneria* stigma projecting above the water happen to be the landing-place, then the skiffs lie alongside, and it necessarily follows that some of the pollen-cells remain hanging on the marginal fringes of the stigmatic lobes. Transference by the wind of adhesive pollen carried on boats formed from floral leaves, is at present known to occur not only in the widely distributed species *Vallisneria spiralis*, but also in *V. alternifolia*, a native of tropical Asia, in *Enalus acoroides* of the Indian and Pacific Oceans, in *Hydrilla verticillata*, and in *Elodea canadensis*, as well as in a few species of the genus *Lagarosiphon* occurring at the Cape and in tropical Africa; only thirteen species in all, belonging to the small family of Hydrocharidaceae.

According to this account of Kerner, the species just named form, in respect of their floral arrangements, a transition to the next group.

II. WIND-POLLINATED PLANTS, ANEMOPHILAE (An).

Sprengel ('Entd. Geheimn.,' pp. 29-32) long ago set forth the characteristic peculiarities of wind-pollinated flowers (see p. 7). In insect-pollinated plants the pollen-grains are sticky, and their exterior is studded with knobs, spines, or other projections, facilitating adhesion to the body of an insect; the relatively small stigma also possesses a sticky surface. But in wind-pollinated plants the pollen-grains are smooth, dry, and dust-like, so as easily to be blown about; the branches of the stigma are richly provided with brush-like or feathery outgrowths, this being a special adaptation for catching the wind-borne pollen, which is produced in very great abundance. Nor do wind-pollinated flowers need any means of allurement, and therefore possess no showy parts, but are inconspicuous, odourless, and devoid of nectar¹. The anthers are loosely suspended from the tips of the long thin filaments (see Fig. 9), or else the whole male inflorescence is in the form of an easily movable catkin. More rarely the individual flowers are pendulous,

¹ A few wind-pollinated flowers, e.g. *Plantago media*, are conspicuous to a certain extent, and receive a corresponding amount of attention from insects. I have described these as wind flowers ('Blütenbesucher,' i, p. 9); they form a transition to insect flowers. The more conspicuous they are, the more numerous are the visits of insects. *Melanostoma mellina* L. shows in the highest degree a special preference for wind-pollinated plants (such as: *Anthoxanthum odoratum* L., *Phleum pratense* L., *Alopecurus pratensis* L., *Poa annua* L., *Festuca pratensis* L., *Agrostis alba* L., *Scirpus palustris* L., *Artemisia Dracunculus* L.). The untiring and ubiquitous honey-bee also seeks out as booty the pollen of many wind-pollinated plants, which occurs abundantly in still weather. The more conspicuous species of *Plantago* are also sought out by humble-bees, and on the wind flowers of *Plantago media* L. may be seen a mixed gathering of bees, flies, and beetles (op. cit., p. 10).

and movable by the wind; still more rarely the flowers, or floral parts, are quite immobile, or the anthers are explosive (cf. Delpino's groups, p. 62).

Wind-flowers are also dichogamous or diclinous, so that self-pollination is entirely or partly prevented.

A great many of our trees and shrubs, indigenous or introduced, that flower in spring, are pollinated by the wind, e.g. hazel (*Corylus Avellana*), alder (*Alnus*

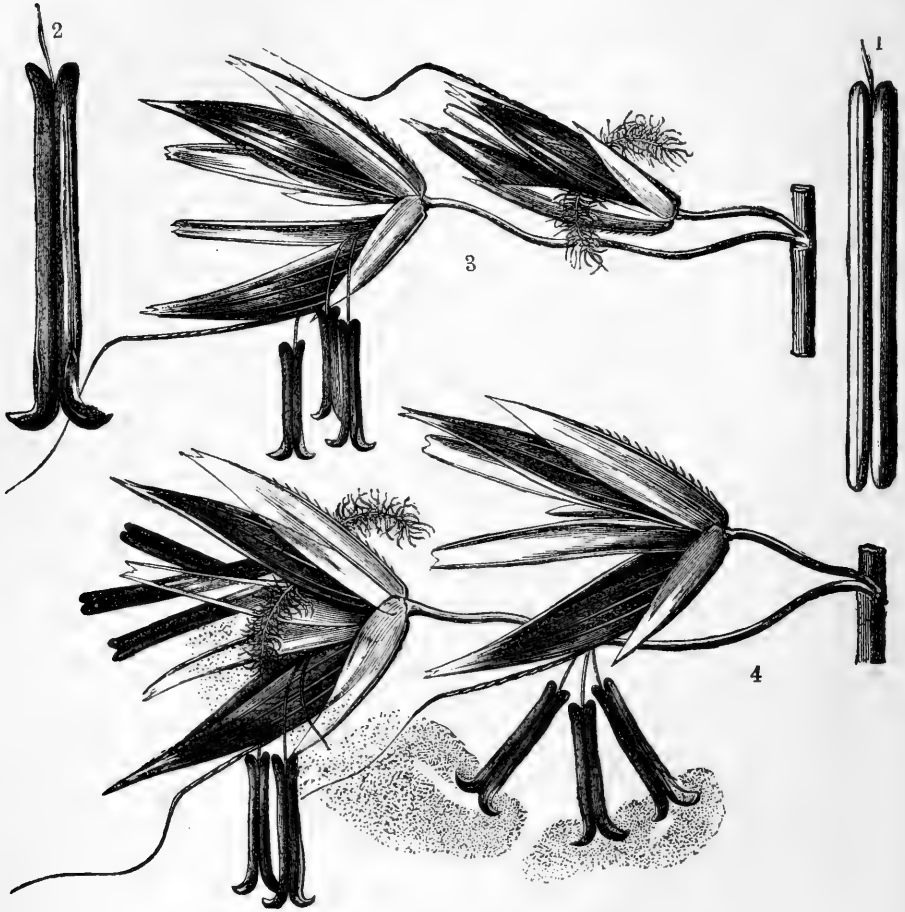


FIG. 9. *Arrhenatherum elatius*, M. et K., a wind-pollinated plant. (1) A closed anther. (2) A dehiscent anther. (3) Spikelet with widely opened glumes, and anthers hanging down in still air. (4) Spikelet exposed to wind. The pendent anthers of one flower are discharging pollen; the anthers of another flower are empty; one anther has dropped from its filament; the anthers of a third flower that is still closed are just beginning to protrude. (1) and (2), $\times 12$; (3) and (4), $\times 5$. (After Kerner.)

glutinosa and incana), elm (*Ulmus campestris*, *montana*, and *effusa*), plane (*Platanus orientalis* and *occidentalis*), walnut (*Juglans regia*), beech (*Fagus sylvatica*), oak (*Quercus pedunculata*, *sessiliflora*), hornbeam (*Carpinus Betulus*), birch (*Betula verrucosa*, *pubescens*, *humilis*, *nana*), poplar (*Populus alba*, *tremula*, *nigra*, *molinifera*, *balsamifera*), ash (*Fraxinus excelsior*), and others. Well-marked cases of wind-pollina-

tion are also found in all the Grasses, Cyperaceae and Juncaceae, and in species of the genera *Potamogeton*, *Triglochin*, *Rumex*, *Chenopodium* (?), *Plantago*, *Littorella*, *Hippuris*, *Myriophyllum*, and all the Gymnosperms.

Kerner ('Nat. Hist. Pl.,' II, p. 129) was the first to call attention to the fact that some flowers otherwise possessing well-marked entomophilous characters, are at times wind-pollinated. Some of the *Rhinanthaceae* and *Ericaceae*, according to him, are insect-pollinated during the early part of their flowering period, but wind-pollinated later on. The flowers of *Bartsia*, *Lathraea*, *Calluna vulgaris*, and *Erica carnea*, are so constructed that when the flowers have just opened, a dispersal of the pollen by wind is impossible; at this time, during fine weather, the flowers are visited by numerous nectar-sucking insects, which effect crossing. 'Later on the arrangement is precisely the opposite; the supply of nectar is exhausted, and insects stop away. But, on the other hand, the filaments elongate considerably, so that the anthers are pushed out of the opening of the corolla, the pollen contained in them is discharged, and at the proper time conveyed by the wind to the stigmas of younger flowers. The study of these plants conveys the impression that a second apparatus is prepared lest the first should fail, so that in any case the object of flowering may be attained, and this is in fact necessary. For it may easily happen that owing to unfavourable weather the visits of insects may for a long time be few in number, or fail altogether. In such cases, in most plants, provision is made that flowering may not take place in vain.' (Kerner, *op. cit.*)

F. Hildebrand (*Ber. D. bot. Ges.*, Berlin, xv, 1897) drew similar conclusions from the study of species of *Cyclamen*. These also are successively adapted for pollination by insects and wind. In the first (entomophilous) floral condition, the pollen-grains of the cyclamens are made sticky by an oily covering, but later on (in the anemophilous condition of the flowers) they become powdery, as the stickiness of the oil disappears.

True wind flowers become more numerous as regards individuals and species with increasing exposure of their habitat to the wind. As I have proved in my work, '*Blumen und Insekten auf den Halligen*' (p. 11 [51]), the anemophilous plants of the German flora constitute about 21.5% of the whole, those of the flora of Schleswig-Holstein about 27%, while those of the Islands Röm, Sylt, Amrum, and Föhr, which are exposed to the constant west winds from the North Sea, and to the westerly storms that rage over them, amount to 36.25%. On the Halligen, small, flat, crowded, marshy islands, that at ordinary tides project little more than a metre above the level of the North Sea, and over which the wind rushes unceasingly without finding anything to resist it, the proportion of anemophilous flowers even rises to 47%. The above rule was confirmed by my investigations of the floral arrangements of the plants of Heligoland. On the west side of the high land, which is most exposed to storms, wind-pollinated plants are dominant, while on the eastern declivity of this region, which in parts lies 20-24 metres lower than the western margin, insect-visitors find a certain amount of shelter from the raging westerly storms, and consequently entomophilous plants occur here in greater abundance, while anemophilous species are less numerous (*cf.* Knuth, '*Bl. u. Ins. auf Helgoland*,' p. 5 [26]).

As pollen is easily spoilt by moisture, provision is found for protecting it from damp: e.g. the versatile anthers of grasses, &c., only open in dry air, so that the probability of wetting is small. Among the pendulous catkins of alders, hazels, birches, poplars, hornbeams, &c., the anthers are sheltered under shield-shaped covering-leaves. According to Kerner ('Nat. Hist. Pl.,' Eng. Ed. 1, II, p. 148) the pollen of the trees and bushes just named, after actual discharge from the anthers, is not at once scattered through the air. It is at first heaped in some place in or near the flower that is sheltered from moisture, and thence it is blown by the wind only when the environmental conditions are most favourable for its distribution. In the plants named, the dorsal side of the flowers serves as temporary storing-place for the pollen; among the pines, firs, and spruces (op. cit., pp. 145-8) it is the excavated dorsal side of the stamen immediately below; in the case of the yew it is the shield-shaped connective, just as in *Juniperus*, *Cupressus*, *Thuja*, *Platanus*.

In *Hippophaë rhamnoides* (op. cit., p. 148) the pollen is concealed in two shell-like investing leaves that meet above, but are open at the sides. Among the species of *Potamogeton*, the pollen falls during quiet weather into an excavation of the flower-leaf situated below the anthers. In *Triglochin* the pollen falls, as I have shown, into the crescentic or boat-shaped pockets that represent the perianth-leaves, and which are situated under the anthers; from these it is scattered even by the lightest breeze ('*Blumen und Insekten auf den nordfriesischen Inseln*,' p. 136).

Far more numerous and more interesting adaptations for the protection of pollen than those possessed by anemophilous flowers are found among the more highly developed entomophilous flowers, since shelter for their smaller quantity of pollen is a pressing necessity.

III. ANIMAL-POLLINATED PLANTS, ZOIDIOPHILAE (Z).

(a) Plants with Bat-pollinated Flowers, Chiropterophilae (Ch).

The first observed case of flowers pollinated by bats was described by W. Burck, in the *Annals of the Botanic Gardens at Buitenzorg* (1892)—a *Freycinetia* (Pandanaceae) that occurs in Java, and which climbs to the very highest parts of the tree that supports it, develops several times a year a number of large flowers of a delicate rose colour, which look very conspicuous among the long, dark-green leaves. Many of the flowers are found lying on the ground, and from these it appears that the plant is dioecious. In both male and female flowers the three inner-coloured structures that play the part of petals are devoured by a bat, the Kalong, or Flying-fox (*Pteropus edulis*). While this animal is eating these alluring structures of the male flower, it touches the pollen-covered anthers with its hairy head, and when visiting a female flower transfers to the stigma the pollen thus received. Until it is observed that the transference of pollen is otherwise effected, it must be assumed that the apparent devastation which the Kalong effects among the flowers of the *Freycinetia* serves the useful purpose of pollination, so that the plant must be described as bat-pollinated.

Plants that are pollinated by bats have also been observed in Trinidad. In the *Bulletin of Miscellaneous Information of the Royal Botanic Garden at Trinidad*, ii, part 3, No. 10 (April, 1897), pp. 30, 31, J. H. Hart, Superintendent of the

Garden, makes a communication regarding the pollination by bats of an indigenous species, *Bauhinia megalandra* (sp. nov.). The tree has a height of about 10 metres. Its long white flowers bloom in the evening hours, from about four to six o'clock. (Darkness sets in about six o'clock at the season when this plant is in flower (January) in Trinidad.) About half an hour previously bats of various species may be observed flying with great rapidity from flower to flower, and it can be observed that their visits are immediately followed by the fall of the white petals to the ground. If the tree is examined next morning, not a single complete flower will be found, all of them being more or less torn, and robbed of their long white petals and stamens. When a bat settles on a flower, it holds fast by the projecting stamens, apparently seizing the erect recurved petals, for these are completely scratched or broken to pieces, or else torn off. The stamens are often broken off short at their bases, but the stigma seems to be seldom injured.

There does not appear to be any secretion of nectar, and it is therefore probable that the bats visit the flowers for the sake of such insects as are attracted by the odour of the flowers. In order to capture these insects, the bats occupy such a position in the flowers that they effect pollination.

Mr. J. H. Hart supplements these observations in a letter to me, pointing out that the flowers of yet another tree, *Eperua falcata* ('Wallaba') are visited by bats. *Glossonycteris Geoffroyi Gray*, a species in which the brush-like tongue resembles that of a humming-bird, was captured on the flowers of *Eperua* in the Botanic Gardens at Trinidad. Its behaviour when visiting the flowers is so like that of moths, that at first it was taken for one of them. There can be no doubt that it pollinates the flowers of this tree (cf. P. Knuth, 'Neue Beobachtungen über fledermausblütige Pflanzen,' Bot. Centralbl., Cassel, lxxii, 1897).

(b) Plants with Bird-pollinated Flowers, Ornithophilae (O)¹.

Plants in which the flowers are pollinated by birds (humming-birds, honey-suckers, rarely sparrows) are found in the tropics.

The first observations on the regular visits of birds to flowers in tropical America belong to the first half of the eighteenth century. The descriptions and illustrations ascribed by Kronfeld (Bot. Centralbl., I, 1892, pp. 290-4) to the gardener Franz Boos, are taken, according to Loesener (Bot. Centralbl., li, 1892, pp. 138, 139), from a work by Catesby ('Natural History of Carolina, Florida, and the Bahama Islands,' 1731).

About a century and a half elapsed before another and larger work gave a thorough account of the visits of humming-birds to flowers. In his celebrated book, 'The Naturalist in Nicaragua' (London, 1874), Thomas Belt cites the pollination of *Marcgravia nepenthoides* by humming-birds as a notable example. This is a climbing plant that ascends to a great height, and possesses pendulous, long-stalked flowers arranged in a circle. A prolongation of the axis of the

¹ After the completion of this part of the manuscript I received a work by my botanical friend Professor E. Loew, 'Über ornithophile Pflanzen' (from 'Festschrift zum 150jährigen Bestehen des Königl. Realgymnasiums zu Berlin,' 1897). In this work the material involved is treated in an exhaustive manner.

inflorescence bears a number of pitcher-shaped nectaries, with their openings turned towards the flowers. The fluid contained in these receptacles is sought out by insects, which in their turn attract numerous insectivorous birds, many species of humming-bird being among them. These touch with their backs the pendulous anthers, brush off the pollen, and transfer it to the stigma when they visit another flower (cf. Fig. 10).



FIG. 10. *Marcgravia nepenthoides*, Seemann, a Humming-bird flower. (After Wittmack.) A, Nectaries.

Another interesting example of the pollination of flowers by birds, and one that brings to mind the way in which *Freycinetia* rewards the bats which transfer pollen, is published by Fritz Müller (*Kosmos*, i, 1886, pp. 93-8);—the flower of *Feijoa*, a tree belonging to the family *Myrtaceae*, and common in the Brazilian highlands, possesses fifty to sixty very firm and stiff blood-red stamens producing bright yellow pollen, and a rigid dark-red style, which tapers above, and bears a capitate stigma projecting beyond the whorl of stamens. There is no nectary. Above the four sepals, which are coloured red on the inner side, there are four petals which at first display their coloured outer surfaces. They increase in diameter from 15 to 25 or 30 mm. Soon they roll up in such a way

that their coloured outer surfaces are covered, while the dazzling white inner surfaces are visible from afar. These rolled petals are fleshy, and have a sweet taste, while the young petals before rolling up are either tasteless or acrid.

Fritz Müller states that the beautiful flowers of *Feijoa* are scarcely ever visited by bees. On the other hand, according to the observations of Hans Lorenz (Fritz Müller's grandson, then five years old), the petals, which are rolled together like omelettes, ready for a bite, are readily devoured by black and brown birds (probably males and females of species of *Thamnophilus*), which in the process first of all come into contact with and pollinate the prominent stigma, and then brush against the pollen-covered anthers, thus covering themselves with a fresh supply of pollen.

E. Ule has made a similar observation regarding a myrtle-like Brazilian shrub: the petals, which taste like orange-sugar, are barely 5 mm. long, while the purple-red stamens are almost 30 mm. in length.

Fritz Müller has observed that humming-birds effect pollination in numerous other Brazilian plants, such as species of *Salvia*, *Rubiaceae*, &c., and more especially also in South Brazilian species of *Abutilon*.—‘A large and beautiful humming-bird, the black breast of which shines like a glowing coal whenever the bird is in any way excited,’ writes Fritz Müller on August 26, 1871, to his brother Hermann, ‘has, with his inconspicuous wife, made himself almost completely master of the abutilons in my garden, and drives away all other species. All flowers that are not under cover are pollinated by him.’

Fritz Müller writes to F. Ludwig with regard to humming-birds and other species as agents of pollination (Bot. Centralbl., lxxi, 1897, pp. 301, 302), to the following effect.—‘Humming-birds, which constitute one of the most important groups of pollinators, are on the wing in Brazil throughout the year. Their activity in visiting flowers is far greater than would appear from accounts known to me. I could almost believe that the list of flowers not visited by them would be considerably smaller than a list of those that are visited. Even quite inconspicuous flowers, such as those of the small Composite—*Buddleia brasiliensis*—and the little green blossoms of *Hohenbergia angusta*, are visited by them. In the winter months, when butterflies and bees are very rare (except the social species of *Melipona* and *Trigona*), these birds are almost the only flower-visitors. Frequently (like the largest of our bees, a *Xylocopa*) they steal the nectar by boring, e.g. in *Abutilon* and the beautiful *Jacaranda (digitaliflora?)*.’

The flower-visiting humming-birds are often so like the hawk-moths, which seek out the same flowers, as to be mistaken for them: ‘Several times,’ says Bates (‘The Naturalist on the River Amazon,’ London, ed. 1892, p. 94), ‘I shot by mistake a humming-bird hawk-moth instead of a bird. This moth (*Macroglossa Titan*) is somewhat smaller than humming-birds generally are; but its manner of flight, and the way it poises itself before a flower, whilst probing it with its proboscis, are precisely like the same actions of humming-birds. It was only after many days’ experience that I learnt to distinguish one from the other when on the wing’ (cf. Fig. 11).

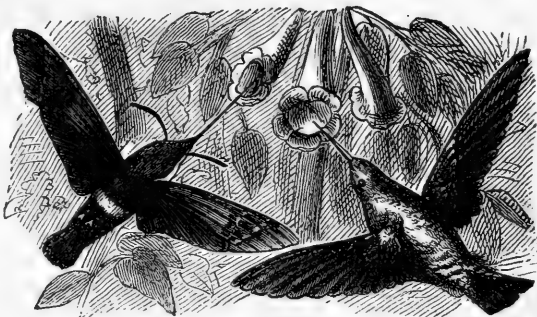


FIG. 11. *Humming-Bird* and *Humming-bird Hawk-moth* (Herm. Müller, after Bates.)

Fritz Müller made the same observation in Brazil. He wrote as follows to his brother Hermann: ‘A large bush of a beautiful sky-blue *Salvia*, that occurs here, and which is now blooming in my garden, is visited by a *Macroglossa*, which has such a deceptive likeness to a humming-bird in form, colour, and mode of flight, that my little ones described it to me as a remarkable six-legged humming-bird.’

The only humming-bird that occurs in North America¹ is *Trochilus colubris*, which is best known as the pollinator of *Impatiens fulva*. According to Asa Gray, Beal, Robertson, and Trelease, it also pollinates many other flowers, such as *Tecoma radicans*, *Hibiscus lasiocarpus*, *Lobelia cardinalis*, *Gossypium herbaceum*, *Fuchsia*, *Bignonia*, *Passiflora incarnata*, *Aesculus parviflora*, and others, as well as acclimatized European species, such as *Scrophularia nodosa*, *Trifolium pratense*, and *Oenothera*

¹ [This statement is incorrect. Newton (‘A Dictionary of Birds,’ ed. 1899) states (p. 448), ‘In the north-west *Selatophorus rufus* in summer visits the ribes-blossoms of Sitka.’ And again (p. 450), ‘Seventeen species have been enrolled in the fauna of the United States . . .’—Tr.]

biennis, which are without exception flowers for which, in Europe, predilection is shown by insects with a long proboscis.' (Cf. Knuth, 'Die Blütenbesucher derselben Pflanzenart in verschiedenen Gegenden,' II.)

Trelease also describes the tropical American forms *Salvia gesneraefolia* and *S. Heerii*, and the Brazilian species *S. splendens* Sello, as ornithophilous, as well as *Erica Willmorei*, which is native to South Africa (Proc. Soc. Nat. Hist., Boston, xxi, 1882).

On Mindanao, one of the Philippine Is., Everett observed (Nature, xvi, 1877) numerous birds of the family Nectariniidae (species of *Loriculus*, &c.), which, without alighting, catch the insects occurring in the recesses of flowers, meanwhile loading the feathers at the base of the beak with pollen.

Evans (Nature, xviii, 1878) saw *Tecoma capensis* pollinated by honey-suckers in Natal. In New Zealand, Thomson (Trans. and Proc. N. Zeal. Inst., Wellington, xiii, 1880) observed the following species to be regularly or occasionally visited by honey-suckers:—*Clianthus puniceus*, *Sophora tetraptera*, *Metrosideros lucida*, *Loranthus Colensoi*, *Fuchsia excorticata*, *Dracophyllum longifolium*, and *Phormium tenax*. In Australia F. v. Müller saw (in 1883) *Grevillea robusta* pollinated by birds (Loew, 'Einführung,' p. 368).

Furthermore, according to E. Galpin (Gard. Chron., ix, 1891) the following Cape plants are ornithophilous:—*Erythrina caffra*, *Tecoma capensis*, *Leonotis Leonurus*, *Halleria lucida*, *Antholyza aethiopica*, and many sp. of *Aloë*. According to M. S. Evans (Nature, li, 1895) both *Loranthus Kraussianus* and *L. Dregei*, in Natal, are visited and pollinated by birds, the former by *Cinnyris olivaceus* and *Barbetula pusilla*, the latter by *Cinnyris Verreauxi*.

According to J. Hancock (Amer. Nat., Boston, xxviii, 1894), the humming-birds (*Trochilus colubris* L.) which visit *Lonicera sempervirens* carry away pollen, especially upon the feathers at the corner of the mouth. The pollen-grains are adapted to this kind of transference.

We are indebted to Scott-Elliot (Ann. Bot., Oxford, iv, 1889-90, pp. 265-80) for numerous recent investigations with regard to the ornithophilous plants of Africa and Madagascar. In his memoir ('Ornithophilous Flowers in South Africa') he mentions honey-suckers of the families Meliphagidae (*Zosterops*), and Cinnyridae (*Nectarinia*, *Cinnyris*) as the sole or occasional pollinators of the following species, the visitors of which are indicated within brackets:—*Melanthus major* L. [visited by *Nectarinia chalybea*], *M. comosus* Vahl [N. famosa], *M. Dregeanus* Vahl [*Zosterops virens*], *Erythrina caffra* DC. [sp. of *Nectarinia*, *Zosterops virens*], *Tecoma capensis* Lindl. [*Nectarinia* Afra, *Zosterops virens*], *Leonotis ovata* Spreng. [*Cinnyris Kirkii*], *Salvia aurea* E. [*Zosterops capensis*], *Protea incompta* R. Br., *P. mellifera* Thunb., *P. longiflora* Lam., *P. Scolymus* Thunb. [all visited by *Promerops caper*], *Leucospermum conocarpum* R. Br., *Antholyza aethiopica* L., *A. praealta* Red., *Babiana ringens* Ker., *Erica fascicularis* L., *E. purpurea* Andr., *E. Plunkenetii*, *Lobostemon montanum* Buck, *Lycium tubulosum* Nees, *Sarcocolla squamosa* Benth., *Scholia speciosa* Jacq., *Sutherlandia frutescens* R. Br., &c.

In another publication—'Note on the Fertilization of *Musa*, *Strelitzia Reginae*, and *Ravenala madagascariensis*' (op. cit., pp. 259-63)—Scott-Elliot shows that the pollination of the plants in question is effected less by insects than by birds, which by

means of their thin, curved beaks can gain access to flowers enclosed by stiff and high leaves much more easily than bees. In Natal, the pollen of *Musa* is usually transferred by the *Cinnyridae*, more rarely by bees. In Mauritius, on the contrary, the bananas are pollinated by insects. Scott-Elliot observed that *Ravenala madagascariensis* and *Strelitzia Reginae* were pollinated by *Nectarinia souimanga* and *Nectarinia Afra*, respectively.

In the last-named plant, numerous threads of one or several cells are distributed through the pollen-masses. They take origin from the epidermis of the anther, and bind the pollen together, so that quite a large quantity can be drawn out at the same time by means of a needle. This is probably a special adaptation, rendering possible the transfer of a large number of pollen-grains to the birds that effect pollination. Considering the relatively large size of such birds, this is a matter of no small importance (cf. E. Palla in *Ber. D. bot. Ges.*, Berlin, ix, 1891, p. 86, and A. Wagner, *op. cit.*, xii, 1894, p. 54).

In the concluding sentences of his last-named memoir, Scott-Elliot, according to Taubert (*Bot. Centralbl.*, xlv, 1891, p. 161), opposes the view expressed by Wallace, that the colours of flower-visiting birds bear no relation to their habits, and shares Darwin's opinions that they present a certain amount of adaptation to the plants they visit. His conclusions are based on the fact that the breasts of most *Cinnyridae* possess a characteristic red hue, corresponding exactly to the colour observed by him in most South African ornithophilous flowers, a colour which is also constantly present among *Labiatae*, *Leguminosae*, *Iridaceae*, and others, when these are pollinated by birds.

Humming-birds and honey-birds, however, are not the chief or exclusive agents of cross-pollination in many flowers. According to the reports of Fritz Müller to his brother Hermann (Schenck's '*Handbuch der Botanik*,' I, p. 17), there are also larger birds that do this:—the large flowers of *Carolinea*, with their immensely long filaments, are not pollinated by humming-birds, which are much too small, but by woodpeckers and other relatively large forms. Hermann Müller further remarks (*op. cit.*), 'Woodpeckers may seek in the flower for insects as well as honey, but certainly for the latter; since, when they peck oranges, as is frequently the case, they can, of course, expect only sweet juice, and not insects.'

It therefore appears that in the tropical and sub-tropical zones there are numerous flowers that are visited by birds, with consequent pollination. Owing to the incompleteness of the material, no grouping of the manifold adaptations is at present possible. In Europe, the visits of birds to flowers occur only exceptionally, and, when they do, pollination does not take place by way of recompense, for the birds only work havoc. Thus, Hermann Müller (*Nature*, ix, 1874, pp. 482, 509; x, 1874, pp. 6, 24; xiii, 1876, p. 427; xv, 1877, p. 530; xvi, 1877, pp. 8, 41, 84, 163) saw sparrows pecking off the flowers of the yellow crocus, and bullfinches 'biting out of primroses with hereditary skill exactly that section of the lowest part of the flower which contains the nectar.'

(c) **Plants with Snail-pollinated or Slug-pollinated Flowers,
Malacophilae (M).**

The possibility of snails or slugs effecting pollination arises when small flowers are crowded together at the same level, and in the case of flat flowers with stigmas and anthers which project but little. It is then possible for such creatures when creeping over the flowers or inflorescences, to transfer pollen-grains which remain clinging to the slimy surface of their foot to the stigmas of the same plant, or even to those of others. In most cases, however, snails or slugs are only the occasional and not the exclusive agents of pollination.

The first contribution to our knowledge of malacophilous plants was made by Delpino ('*Ulter. osserv. sulla dicog. nel regno veg.*,' *Atti Soc. ital. sc. nat.*, Milano, xi and xii, 1868 and 1869, pp. 238-40) when he described the pollination of *Rohdea japonica* (? *Asparagineae*) by *Helix aspersa*, *H. vermiculata*, and others. Hermann Müller ('*Fertilisation*,' p. 551) summarizes the passage as follows:—'This plant seems to be transitional to the *Aroideae*, for it possesses a kind of spadix with crowded, flattened flowers arranged in an unbroken spiral. The flattening of the margin of the perianth to exactly the same level as the tips of the anthers and stigmas led Delpino to suspect pollination by animals creeping over the flowers, and he actually observed snails (*Helix aspersa*, *vermiculata*, and others), each of which consumed greedily the yellow perianth, which is fleshy at the time of flowering, of about ten flowers belonging to any particular spadix, and then visited another inflorescence. Only the flowers touched by snails were fertile; the plants appeared infertile as regards their own pollen. There can be no doubt from these observations that snails are active agents of pollination.

Delpino (op. cit., pp. 235-8) suspected that *Alocasia odora* is also pollinated by snails; the entire length of spadix, according to Hermann Müller's paraphrase ('*Fertilisation*,' p. 564), is beset with normal and reduced female and male flowers. Only the female flowers are enclosed in the lower dilated part of the spathe, and they are the first to ripen. There is only a narrow passage by which snails can creep into the space surrounding the stigmas, into which they are tempted by the diffusion of an agreeable odour. Even this entry is closed in the second stage of flowering, at which time the anthers dehisce. Snails which visit flowers that are in this second stage seek admission in vain, covering themselves however with pollen, which they deposit on the stigmas of younger flowers to which the approach still stands open. After the snails have discharged the important work of cross-pollination, Delpino states that they are killed by means of an irritant juice in the space that encloses them, being thus prevented from devouring the flowers.

Delpino also supposed that there was occasional transfer of pollen by snails in *Amorphophallus variabilis*, species of *Anthurium*, *Arisaema filiforme*, *Atherurus tripartitus*, and *Typhonium cuspidatum*.

Ludwig (Kosmos, vi, 1882, pp. 34 et seq.) observed and investigated at Greiz-greenhouse specimens of *Philodendron pinnatifidum Schott.*, and believes that this plant is pollinated by snails. The entire floral arrangement agrees in many points with that of *Rohdea japonica* and *Alocasia odora*, which Delpino has described as snail-pollinated. Ludwig points out that in *Philodendron pinnatifidum* self-pollina-

tion is out of the question, and that pollen can only be transferred by snails.

Warming (Jahrb. Bot., Leipzig, iv, 1883, pp. 328-40), who made his observations at Lagoa Santa, traverses this view and argues that snail-pollination is impossible owing to—

1. The rarity of snails in the locality mentioned (Lagoa Santa).
2. The isolated occurrence of the plant there.
3. The short flowering period, and the extremely rare occurrence of several spadices blooming on the same plant.
4. The discharge of carbonic acid gas observed by Ludwig within the spathe.

Warming establishes the fact that at the time of pollination a sticky juice is secreted, so that even dry-bodied animals can effect pollination. He is of opinion that fertilization is effected by pollen of the same spadix.

In opposition to this view of Warming, Ludwig holds (Kosmos, i, 1884) that the observations of the former were carried out in a place where the plant occurs very sporadically in the tops of tall forest trees, and therefore not in sufficient abundance to attract the characteristic agents of pollination.

Ludwig accepts the supposed occasional malacophily of our native Lemnaceae: snails (and insects) wandering about on the patches of duckweed break off pollen-grains and bring them to the concave stigmatic surface. This plant does not need to employ any special allurement; without any display, and without any other inducement than a firm substratum, it achieves what 'flowers' achieve by beauty, honey, pleasant odour, &c., which at times serve to attract unbidden guests. Duckweeds like Aroids (according to Stahl, 'Pflanzen und Schnecken,' Jena, 1888) are protected by raphides against the attacks of snails (cf. Ludwig, 'Lehrbuch der Biologie der Pflanzen,' p. 544).

In a few European species pollination by snails actually occurs as well as pollination by insects. E. Warming (Bot. Tids., Kjöbenhavn, ii, 1877) observed, for instance, that the inflorescences of *Calla palustris*¹, which are chiefly visited by small flies, are also frequented by snails which, crawling up on several inflorescences placed one behind the other, transfer pollen-grains that have stuck to the slimy surface of their foot to the stigmas of other plants. Hermann Müller observed ('Fertilisation,' p. 246) something similar in the case of *Chrysosplenium alternifolium*. Besides flies, beetles, and ants, he found on numerous flowers small snails (Succinea), some creeping about, others devouring styles or stamens. Pollen-grains were usually to be found in the slimy tracks that occurred on the flowers, and in several cases it was obvious that pollen had been transferred to the stigma by snails. Ludwig (SitzBer. Ges. natf. Freunde, Berlin, 1889, pp. 16-18) observed that Chrysan-

¹ In the garden of the Ober-Realschule at Kiel, I observed (on August 4, 1897) a young specimen of *Helix hortensis* on the flowers of the species described as *Calla maculata*. The snail crawled about on the inflorescence, and examination of its foot showed the presence of pollen-grains, so that the possibility of the transference of pollen by snails is proved for this Aroid too. I observed at the same place (on September 23, 1897) the small slug *Limax cinereus* (?) among the flowers of *Colchicum autumnale*. It devoured the perianth leaves, and in doing so occasionally disturbed anthers and stigma, so that self- or cross-pollination might result. Numerous flowers were almost completely deprived of their perianth by slugs, so that frequent visits may be inferred.

themum leucanthemum was visited by a small slug (*Limax laevis* Müll.) which in wet weather discharged the task of pollination. In one small area Ludwig found this slug on hundreds of capitula, and it seemed as if the white ray-florets formed the attraction, as they were very greedily devoured by the visitors. Ludwig thus comments on this observation:—‘It proves that plants which lack the customary agents of pollination, when continuous rain occurs during the flowering season, and would otherwise produce no fruit, may find in slugs effective substitutes for insects, which are only active in dry weather.’ Other botanists have repeatedly observed that snails and slugs visit and pollinate flowers, e.g.:—Engler (‘Monogr. Phanerog. auct. A. et Cas. de Candolle,’ V, 2, p. 30) substantiates this for *Anthurium coriaceum* and *A. martianum*, as he observed small slugs visiting them in the aquarium of the Botanic Garden in Munich. Trelease (Amer. Nat., Boston, xiii, 1879), in North America, saw small snails carrying pollen about on *Symplocarpus foetidus* Salisb.

(d) Plants with Insect-pollinated Flowers. Entomophilae (En).

In his ‘Das entdeckte Geh.’ (pp. 9–21) Sprengel has set forth the essential characters of insect-pollinated plants (cf. p. 5). An exhaustive account is therefore superfluous, and having regard to the present state of our knowledge, it will only be necessary to emphasize the most important points.

In contrast to the dusty pollen of wind-pollinated plants, for which the name ‘flower dust’ is very appropriate, insect-pollinated flowers possess adhesive pollen. Its outer coat is beset with small spines, warts, pits, grooves, needle- or hair-like structures, in short, with numerous small processes by which its adhesion to the bodies of visitors is specially favoured. At times the pollen-cells are bound together by threads of a delicate sticky substance known as *Viscin*, by which adhesion is rendered still easier. Such threads of *viscin* occur, e.g. on the pollen-grains of *Oenothera*, *Epilobium*, and other *Onagraceae*, among species of *Rhododendron*, &c.

The size of pollen-grains varies greatly. It is mostly given in micromillimetres ($1\ \mu = 0.001\text{ mm.}$). Thus, according to Kerner (‘Nat. Hist. Pl.,’ Eng. Ed. I, II, p. 97), the size in *Myosotis alpestris* is 0.0025–0.0034 mm., in *Mirabilis Jalapa* 0.22–0.25 mm., so that in the latter plant it is a hundredfold that of the former. The average size is about 25–100 μ .

The pollen of all flowering plants, hydrophilous forms alone excepted, is at once damaged by water. Kerner has paid special attention to the many ways in which pollen is protected. I therefore enumerate the protective arrangements as distinguished by him (‘Nat. Hist. Pl.,’ Eng. Ed. I, II, pp. 104–29).

1. The anthers are covered by a protective roof. This is effected in one of the following ways:—

(a) Campanulate, urceolate, basin-shaped, or cup-shaped flowers, depending from curved stalks, e.g. species of *Calluna*, *Vaccinium*, *Campanula*, *Pulmonaria*, and *Convallaria*; *Atropa Belladonna*; species of *Galanthus*, *Leucojum*, and *Fritillaria*.

(b) Curvature of the main floral axis; the flowers are thus inverted as before, so that the stamens are sheltered by the petals:—*Berberis*, *Prunus Padus*.

(c) The flowers or inflorescences bend over periodically, their stalks (or the elongated inferior ovaries) curving downwards at night and in bad weather, so that once

more the anthers come under the shelter of the petals :—*Campanula patula*, *Geranium Robertianum*, *Anemone nemorosa*, *Stellaria graminea*, *Solanum tuberosum*, *Polemonium coeruleum*, *Scabiosa lucida*, *Bellis perennis*, *Doronicum*, *Sonchus*, *Tussilago*, *Astrantia alpina* and *carniolica*, *Sisymbrium Thalianum*; *Epilobium montanum*, *hirsutum*, *roseum*, and many others.

(d) *The flowers are sheltered under foliage leaves*:—*Limes*, *Impatiens Noli-tangere*, *Daphne Laureola*, *Althaea rosea*, and others.

(e) *The inflorescences are roofed over by a large spathe*:—Many Aroids.

(f) *The petals close together above the stamens*:—*Trollius europaeus*.

(g) *The opening of the flower is lateral*:—Many Labiates, *Pinguicula*, *Alectorolophus*, *Melampyrum*, *Euphrasia*, *Viola*, *Aconitum*, and others.

(h) *The flowers are entirely closed*:—All Papilionaceae, *Corydalis*, *Linaria*, *Antirrhinum*.

(i) *The stigmas form a protective roof over the anthers*:—*Iris*.

(k) *The ligulate florets of Composites protect the pollen*:—*Lactuca*, *Hieracium*, *Lapsana*, *Cichorium*.

(l) *The pollen is enclosed in an anther-tube*, from which it is only discharged by a shortening of the filaments when these are disturbed by insect-visits:—*Onopordon*, *Centaurea*.

2. The corolla-tube of funnel-shaped flowers is contracted at the opening, so that no drops of water can enter:—Species of *Phlox*, *Daphne*, *Androsace*, and *Aretia*.

3. The flowers or inflorescences close in unfavourable weather.

(a) *The ligulate ray-florets, or the involucrel bracts close over the disk-florets*:—*Carlina*.

(b) *The whole flower closes in dull or rough weather*:—*Colchicum*, *Crocus*, *Erythraea*; species of *Gentiana*, *Campanula*, and *Ornithogalum*; paeonies, roses, *Datura Stramonium*, *Nymphaea*, *Eranthis*, *Anemone*, *Eschscholtzia*.

4. The anthers that have dehisced in dry weather close up again in moist weather:—*Plantago*, *Globularia*, *Alchemilla*, *Laurus nobilis*, *Thesium*, *Bulbocodium*, *Thalictrum*, *Vitis*, *Liriodendron*, *Cistus*, and others.

5. The pollen-grains are covered with pits, sufficiently deep to prevent the air contained in them from being driven out by water, so that it forms a layer protecting the pollen-grains from being wetted:—*Cobaea*.

In many plants several of these protective devices are present. Most of the arrangements for the protection of pollen are otherwise advantageous, especially with regard to the possibility of self-fertilization, and the protection of nectar.

A. Hansgirg (SitzBer. Böhm. Ges. Wiss., Prag, xxxiii, 1896) describes as *ombrophobous* (rain-fearing) such flowers as are able by special movements (ombrophobous movements) to protect themselves against the injurious effect of rain or continued wetting; flowers that are not able to execute such movements he terms *anombrophobous*.

The ombrophobous plants of temperate regions belong to the Xerophytes. The ombrophobous movements cease as soon as the protection of nectaries or

anthers so secured becomes unnecessary, e. g., when the pollen has been discharged from flowers that have opened.

Hansgirg distinguishes four types:—

Type I.—Plants with flowers which open in fine, but close in wet weather, so that penetration of drops of rain is rendered difficult or impossible. The flowers or capitula are borne on stiff stalks which do not change their position, being unable to execute ombrophobous curvatures.

Examples:—Liliaceae (sp. of *Erythronium*, *Tulipa*, and *Ornithogalum*; Iridaceae (*Crocus*, *Sisyrinchium*, *Romulea*); Amaryllidaceae (*Sternbergia*); Colchicaceae; some Gramineae and Juncaceae. Among Dicotyledones:—Compositae (*Helipterum*, *Catananche*, *Sphenogyne*, *Venidium*, *Hymenostoma*, *Tragopogon*, *Crepis*, *Hypochaeris*, *Anisoderis*, *Hieracium*, *Centaurea*, *Carlina*, and others); Campanulaceae (sp. of *Specularia* and *Campanula*); Gentianaceae (*Gentiana*, *Erythraea*); Polemoniaceae (*Gilia*, *Collomia*, *Leptosiphon*); Solanaceae (*Mandragora*, *Datura*); Ficoideae (*Mesembryanthemum*); Ranunculaceae (sp. of *Paeonia*, *Eranthis*, *Trollius*, *Pulsatilla*, *Ceratocephalus*, *Anemone blanda*, and *Ranunculus carpaticus*); Magnoliaceae; Nymphaeaceae; Cactaceae; Cruciferae (*Draba*, sp. of *Arabis*, *Malcolmia*, *Aubretia*, and others); Papaveraceae (*Eschscholtzia*, *Sanguinaria*); Portulacaceae; Rosaceae (*Rosa*, some sp. of *Potentilla*).

Type II.—Plants of which the flowers when open are on flexible erect or obliquely sloping stalks, and have their opening directed upwards. In wet weather they do not close, their pollen, nectar, &c. being protected by special ombrophobous curvatures of the individual flower-stalks, of which the object is to prevent the corolla from being filled with water.

Examples:—species of *Anemone* and *Ranunculus*; *Geum*, *Rubus*, *Fragaria*; Geraniaceae; Papaveraceae; Linaceae; sp. of *Dianthus*; Cruciferae; Leguminosae (*Coronilla*); Saxifraga; Violaceae; Boraginaceae (*Cynoglossum*, *Omphalodes*); Convolvulaceae; Campanulaceae; Polemoniaceae; Solanaceae; Scrophulariaceae.

Type III.—Plants with inflorescences protected from rain by special curving of the main floral axis, or of the axes upon which the capitula, umbels, &c. are borne.

Examples:—many Cruciferae; Fumariaceae (*Corydalis lutea*); Compositae (sp. of *Cenia*, *Emilia*, *Leptosyne*, *Coreopsis*, *Guizotia*, *Lasthenia*, *Ptilomeris*, *Bidens*, *Laya*, *Galinsoga*, and others); and Dipsaceae (sp. of *Scabiosa*, *Cephalaria*, *Pteroccephalus*, and *Knautia*).

Type IV.—Plants with flowers which are erect and open in fine weather, but close on the approach of rain, while they are at the same time protected and turned away from the falling drops of rain by the bending down of the flower-stalk, or of the stalk-like inferior ovaries, the capitular stalks, &c.

Examples:—Liliaceae (*Tulipa*, *Brodiaea*); Campanulaceae; Hydrophyllaceae (*Nemophila*); Polemoniaceae (*Polemonium*); Solanaceae (*Solanum*); Scrophulariaceae (*Veronica*); Convolvulaceae (*Convolvulus*, *Nolana*); Compositae (*Bellis*, *Rhodanthe*, *Sonchus*, and others); Primulaceae (*Anagallis*); many Caryophyllaceae; Oxalideae; Linaceae; Cistineae; Geraniaceae; Onagraceae (*Kneiffia*, *Epilobium*, and others).

Reference has already been made (p. 72) to the various ways in which the pollen of anemophilous plants is protected.

Flowers employ many methods of enticing insects suitable for transferring pollen:—colour and odour, the proffer of pollen and nectar, provision of a shelter, &c.

It is the *petals* or *perianth-leaves* which, owing to their bright colours, play the leading part in bringing about **Conspicuousness** in flowers, and in enticing cross-pollinating insects to visit them. If one side of the corolla is not visible to insects on the wing, it is less brightly coloured than the side which they are able to see. In species of *Gagea* (*G. pratensis*, *arvensis*, *sylvatica*, and others), for instance, the perianth leaves which are spread out like a star in the sunlight, are shining yellow on their inner side, while externally they are of a dull yellow, which is rendered even less conspicuous by a green dorsal stripe. The opposite is true for urceolate or campanulate flowers, such as those of species of *Campanula*, for in these the inner side, which is not seen by insects during flight, is less conspicuous than the outer which is exposed to their view as they wander about in quest of food.

When the petals are modified into nectaries, or have not been fully developed for other reasons, the *sepals* in many cases take over the function that more properly belongs to the petals. This is a very common occurrence, and it may suffice to mention here some *Ranunculaceae*, such as *Anemone nemorosa* and *ranunculoides*, *Hepatica triloba*, *Trollius europaeus*, *Eranthis hyemalis*, *Pulsatilla pratensis*, *Aconitum Napellus*, &c.

The petals are frequently helped by the *sepals* in the work of allurement, so that the two outermost whorls of the flower minister to the same end. The inner side of the sepals in *Nymphaea alba*, for instance, which is turned towards the air and light, is coloured white like the petals, while the under side that lies upon the water and is not visible from above, has a green colour. The inner side of the sepals of *Comarum palustre* is coloured a dark purple brown, so that the flower is made much more conspicuous, for though the petals are similarly coloured, they are only about a third of the size of the sepals.

More rarely the *stamens* serve as a means of allurement. The willows may be cited as the best known examples, their yellow or red anthers enticing numerous insects to visit them. Sometimes filaments are of a bright colour. In species of the genus *Verbascum*, they possess a covering of violet, purple, yellow, or whitish hairs, which is often very conspicuous. Even in the case of *Thalictrum aquilegifolium*, and *Plantago media*, which are anemophilous, the filaments are coloured violet. (Cf. p. 69, note.)

Still more rarely do the *carpels* play the part of alluring agents, e. g., in *Caltha palustris* and *Comarum palustre*.

It more frequently happens that flowers or inflorescences are made more conspicuous by coloured *bracts*, e. g. the purple bracts of *Melampyrum arvense*, the azure-blue ones of *M. nemorosum*, and the blue involucre under the capitulate umbels of species of *Eryngium*, in which even the stalk of the inflorescence is of a bright blue colour.

By the association of several or many flowers in an inflorescence, it is frequently brought about that even small flowers are rendered sufficiently conspicuous. The florets of the *Compositae*, for example, together form inflorescences that are visible from afar, with the result that these plants receive more insect-visits than any

others. The ray-florets are usually ligulate, by which the end in view is attained even more successfully. The enlargement of the marginal flowers of an inflorescence also occurs in the corymbs of some Cruciferae (Iberis), and in many Umbelliferae (Daucus, Heracleum, Anthriscus, Conium, Orlaya, and others).

In many cases there is a division of labour between the flower of an inflorescence: the inner ones are sexual, and devoted to reproduction, the outer are asexual, and have undergone a great development of the parts that serve for attraction, at the expense of stamens and carpels. Instances are afforded by *Centaurea*, *Viburnum Opulus*, and others. It sometimes happens that the upper flowers of an inflorescence serve to attract, while the lower ones are concerned with reproduction. In *Muscari comosum*, for example, the compressed ear-like inflorescence is only a few centimetres in length at the time of budding. Later on, by gradual extension of the axis, it develops into a raceme of 20–30 cm. long, of which the uppermost twenty to thirty flowers remain infertile, but assume a deep blue colour, and are borne upon similarly coloured upwardly directed stalks of 1–2 cm. in length. The (sessile) buds are also blue, but the open flowers with stamens and carpels, about thirty to forty-nine in number, are coloured brown, and arranged in a very loose and inconspicuous raceme (Knuth, 'Blütenbiol. Beob. auf d. Insel Capri,' Bot. Jaarb., v, 1893, pp. 25–7).

Many inflorescences develop flowers on one side only. This is most strikingly seen in racemose inflorescences, e.g. *Digitalis purpurea*, *Teucrium Scorodonia*. If the flowers were arranged regularly around the stem, they would be much less conspicuous than they are when arranged unilaterally, although with this latter arrangement they are only visible to insects coming from one side. Such inflorescences, however, possess the further advantage that their insect-visitors, chiefly bees, ascend them with the greatest regularity, as if on the steps of a ladder, without passing by a single flower, as is very often the case in radially symmetrical inflorescences, with the result that some flowers often remain unfertilized.

J. Urban (Ber. D. bot. Ges., Berlin, iii, 1885, pp. 411 et seq.) calls attention to the fact that one-sidedness in inflorescences is brought about by various causes, namely:—

1. By curvatures of the flower-stalks. This is the case, e.g. in *Digitalis purpurea* L. The bracts and flower-stalks are here regularly arranged around the floral axis; but while the former retain their original position, the latter bend to one side in such a way that the outermost flowers diverge 80–120°, making the inflorescence unilateral. Owing to this arrangement the flowers are adapted for cross-pollination by insects with the least possible loss of time, and visits are secured. They present a striking appearance on one side only, though on this side they are highly conspicuous. This disadvantage is compensated by the fact that the lateral inflorescences developing below the terminal one always turn the side devoid of flowers towards the main axis. Even neighbouring plants are similarly related to one another, for the outer inflorescences turn their flowers outwards, quite independently of the strength or feebleness of the illumination.

In *Scutellaria peregrina* L. and other species of the same genus, the markedly unilateral arrangement of the flowers is chiefly caused by curvature of the flower-stalks, combined with bending of the leaf-stalks.

In *Salvia lanceolata Willd.*, the unilateral arrangement is brought about by twistings and flexures of the flower-stalks only, while the leaves maintain their position. Most of the Orchids develop one-sided inflorescences in a similar fashion.

2. Unilaterality also results from curvature of the flower-stalks in compound inflorescences, e.g. in various species of *Polygonatum* and in *Scrophularia lateriflora Trautv.* As in these species most of the flowers are covered by leaves, and are therefore very inconspicuous, this floral arrangement must either be an adaptation to special agents of pollination, or must have some unknown oecological purpose. A contrast to these cases is afforded by the unilateral inflorescences of *Elsholzia Patrini Garcke*, which also come under this heading, and which are so conspicuous that they are obviously adapted to insect visits.

3. Unilaterality of the inflorescence is conditioned by the nature of the symmetry. The leaves and flowers of all species of *Gladiolus* are primarily distichous. The kind of symmetry possessed, combined with slight torsions and curvatures, produce a markedly one-sided arrangement.

4. Unilaterality of racemes is brought about by suppression of the flowers on one side of the axis. Examples:—species of *Vicia* (*V. pisi-formis L.*, *tenuifolia Roth*, *V. Cracca L.*, and others), also the species of *Lathyrus*, which are admirably adapted to their habitat, and to the visits of insects. If their inflorescences were developed on all sides, the marginal flowers at the back of the cluster would be seldom or never visited by insects.

5. Unilaterality of uniparous cymes, whether these are pure or have arisen by reduction, is characteristic of the *Boraginaceae*, and so forth.

6. Apically unilateral inflorescences include capitula and umbels in the widest sense, and these are characteristic for whole families.

Urban makes the following oecological deduction from his observations:—in a single branching plant, or in several that are near neighbours, the inflorescences turn their flowers outwards in one direction, i.e. away from the centre. The result is a common inflorescence exposed on all sides, and sometimes shared by various individuals. It therefore follows that conspicuousness with reference to insects approaching from a distance is greatly increased, and in the case of inflorescences which have become unilateral by suppression, there is economy of material without sacrifice of conspicuousness. And further, the oecological law for flowers—that the same end can be reached by the most varied means—is equally applicable to unilateral inflorescences.

Conspicuousness is increased in many flowers by *colour-contrast*. This may be exhibited either by single flowers, as in the pansy (*Viola tricolor*), *Linaria Cymbalaria*, *Myosotis palustris*, *Vicia faba*, *Narcissus poeticus*, and others, or it may be between flowers and bracts, e.g. the golden yellow corolla and the deep blue bracts of *Melampyrum nemorosum*; or again the contrast may be between the different flowers of an inflorescence, e.g. the blue ray-florets and the yellow disk-florets of asters, and the like.

It is also a highly remarkable phenomenon that, in some plants, the flowers persist for a considerable time after blooming, assuming a more intense colour than they previously possessed. In this way the conspicuousness of the whole

assemblage of flowers is considerably increased. As Herm. Müller ('Weit. Beob.,' I, p. 299) states, the petals of *Ribes sanguineum*, which are pure white during flowering, become an increasingly darker tint of rose red after the dehiscence of the anthers, the pollination of the stigmas, and the cessation of nectar secretion. The cunning bees however, which play the part of visitors, confine their attention to flowers in which the corolla is still white. In *Ribes aureum* the petals, at first bright yellow, assume a carmine red colour after the stamens and styles fade; thus serving the interests of the community, after their own fertilization has been secured, by heightening the attractions of the whole. Similar relations are observable (op. cit., p. 300) in *Weigela rosea*, *Melampyrum pratense*, *Aesculus Hippocastanum*, species of *Fuchsia*, and others.

According to Fritz Müller (Nature, xvii, 1877, p. 79) there occurs in Brazil a *Lantana* with flowers that are red on the first day, orange on the second, and purple on the third.

According to Ludwig (Biol. Centralbl., vi, 1886) there is a remarkable colour-change in the flowers of *Veronica Sandersoni*. The corolla is at first bright red, while the filaments and style (about 7 mm. in length) are also red. Later on these organs all become white, and the style attains a length of 13 mm.

The most gorgeous example of colour-change (Ludwig, op. cit.) is that seen in the melanostomaceous *Pleroma Sellowianum*, the flowers of which are at first of a pure white, and later on of a purple red. In *Spiraea opulifolia* (Ludwig, op. cit.) the colour continues to change even after fading, becoming most vivid in the ripening capsules. In this case, therefore, the fruits as they mature assist in rendering the plant conspicuous (Just's bot. Jahresber., Leipzig, xiv, (1886) 1888, pp. 806, 807).

Most flowers become inconspicuous as soon as they have been fertilized, assuming a dull colour, and either fading or falling off. The state of things exemplified by the flowers referred to above, is only possible (Ludwig, op. cit., pp. 299, 300) where pollination is effected by a limited set of insects, as otherwise fruitless ransacking of the most conspicuous flowers would mean a great waste of time, delay fertilization, and undoubtedly in many cases create a distaste in the often deceived visitors, so that injury rather than benefit would result. Delpino ('Ult. oss.,' Atti Soc. ital. sc. nat., Milano, xvi, 1874, p. 28) was the first to give an explanation of the colour-change in the flowers of *Ribes aureum*, suggesting that flowers which are over are made conspicuous as such to visitors, which are consequently spared useless work. According to Herm. Müller ('Weit. Beob.,' I, p. 300) such change of colour cannot be the primary significance, for, if it were, flowers exhibiting it would not have the least advantage over those that fade or fall off immediately after pollination. There can be no doubt that the entire floral assemblage is rendered more conspicuous by the persistence and more intense coloration of the fertilized flowers, so that insects are attracted in greater numbers. But obviously such an adaptation can only be of the greatest use if the fertilized flowers are easily to be distinguished from the rest.

Kerner ('Nat. Hist. Pl.,' Eng. Ed. 1, II, pp. 194-5) calls attention to colour-contrast between flowers and the ground. In and around woods the surface in spring is brown or yellow, owing to the fallen leaves of the previous year. The blue flowers of *Hepatica triloba* contrast admirably with such ground. 'On ploughed

land the flowers of *Omphalodes verna* can be seen a hundred yards off over the pale yellow, faded grasses and foliage of the edge of the wood; while at the same distance against a green background they would stand out much less clearly. The same thing is true of many Boragineae, which grow in similar places (*Pulmonaria angustifolia*, *officinalis*, *stiriaca*, *Lithospermum purpureo-coeruleum*), of the lesser Periwinkle (*Vinca minor*), of the Squill (*Scilla bifolia*), and of many others. . . . Above the dark mould of the forest-floor a pale colour, such as that of the Bird's Nest (*Neottia*), of *Monotropa*, and of the Toothwort (*Lathraea*), and other saprophytic and parasitic plants, is plainly visible from a distance. These plants would hardly be noticed in a green meadow.'

I may mention here an investigation which renders it not improbable that there are floral colours which are easily perceived by insects, though the human eye cannot see them. I observed (Bot. Centralbl., xlviii, 1891, pp. 161 et seq.), that the inconspicuous greenish-white flowers of *Sicyos angulata* L. were visited by a very large number of species of bees and flies, although the blossoms present but little contrast to the green foliage leaves and tendrils of the plant. By comparing the action of different floral tints on photographic plates, I showed that *Sicyos angulata* L. is probably of an ultra-violet colour. This would be an analogue to the capacity supposed by Landois to exist in many insects of being able to hear higher tones than the human ear can perceive. In a later publication (op. cit., pp. 314-18) I have demonstrated that in numerous cases where I determined the brightness of the flowers of *Sicyos* (and *Bryonia dioica*) they never equalled three-quarters of the intensity of white, but acted on a photographic plate much more strongly than a rotating disk, which was three-quarters white and a quarter black. This fact can only be explained as due to ultra-violet rays, which are chemically very effective. Perhaps the powerful influence of flowers of *Sicyos* and *Bryonia* on photographic plates is also to be explained by supposing that the numberless smaller glands which cover them act as so many mirrors or lenses receiving and reflecting light, so that their glitter strongly affects gelatine sensitized by silver bromide, and also the optic nerves of insects. At any rate, it seems to be established that the flowers named possess a means of attraction to which the human eye is less sensitive than the eye of insects. Haberlandt ('Eine botanische Tropenreise,' 1893, p. 289) was struck by the innumerable bright yellow flowers of desert plants, which are scarcely to be distinguished from the equally yellow sands of their habitat: 'With regard to the visits of insects, one would expect for the sake of contrast a predominance of blue and violet floral colours.' 'Perhaps we may suppose that ultra-violet floral colours are possessed by desert plants. Their flowers would then appear yellowish only to *our* eyes, and therefore be barely distinguishable from their surroundings' (op. cit., p. 295, note 33).

It may here be remarked that Kerner also has investigated the means of attraction of *Bryonia dioica*, and he explains the almost exclusive visits of a small bee (*Andrena florea*) by supposing that its flowers possess an odour which is perceptible neither to man nor to most insects, but only to the bee in question ('Nat. Hist. Pl.,' Eng. Ed. I, II, p. 206).

The following note by Fritz Müller (Kosmos, iii, 1878, p. 495) may also find fitting place here:—'There is now blooming in this place (South Brazil) one of the

Cucurbitaceae (Trianosperma), of which the countless flowers are odourless, greenish, and quite inconspicuous, while most of them are hidden under the foliage. In spite of this these plants appear to have a quite remarkable power of attracting bees. There is a constant humming and buzzing around them the whole day long; *Apis mellifica* is the chief visitor, and there are also two *Meliponae*. This phenomenon might be explained either by Kerner's hypothesis or by mine.

It is usually impossible to describe the colour of a flower, or at least the shades of colour. Hermann Müller ('Alpenblumen,' p. 502, note) calls attention to the difficulty of representing objectively the colour gradations of flowers. He mentions that Koch ('Synopsis,' ed. tertia, p. 499) depicts the flowers of *Verbena officinalis* as clear purple, while they appear bluish to Müller, and the former calls many other flowers violet which the latter regards as blue. Müller tried therefore ('Alpenblumen,' pp. 562, 563) to imitate as closely as possible by means of Faber's pencils the natural colours of all the flowers he drew, a method which in many cases proved quite satisfactory, though as a rule it attained only very partial success.

In order to represent the hues of flowers simply and accurately, Pillsbury recommends (Bot. Gaz., Chicago, xix, 1894) that six normal colours taken from the spectrum be used as a basis, the proportions in which they are mixed to form any given hue being determined (possibly with black and white) by means of Maxwell's top. Thus, R. 48, V. 52, for *Polygala paucifolia*, indicates that the flowers of that plant contain 48 % red and 52 % violet. With some practice and care the determination may be made with great accuracy.

The most correct method would certainly be to determine floral colours spectroscopically. This, however, is naturally only possible for uniformly coloured flowers. I have frequently attempted such determinations, and did not find them difficult, but the method is certainly not applicable to all flowers. In his work, 'Die Spektralanalyse der Blütenfarben' (Jahrb. wiss. Bot., xx, 1889, pp. 78-105), N. J. C. Müller has spectroscopically analysed the colours of sixty-five different species of flowers, using a micro-spectroscope provided with a micrometer (Seybert's), the illumination being effected by directing the mirror of the microscope towards a bright cloud. The spectra of floral leaves thus obtained show the absorption bands of the pigments (expressed by shading) between the lines of Fraunhofer so clearly, that this mode of representation appears thoroughly adapted for application in making comparisons between different floral colours.

Next to colour, **Odour** is the most important allurement for animals that visit flowers, and in many cases it can scarcely be decided which of the two is the more effective. It is usually the flower that is odorous, but in individual cases the smell of the foliage and of the stem is obviously an attraction to insects. This purpose may be served, for instance, by the strong smell of the leaves of *Ruta graveolens*, as well as that of species of mint, lavender, marjoram, &c.

In some cases there is without doubt a *relationship of mutual exclusion between colour and odour in flowers*, i.e. there are numerous flowers with very gaudy, conspicuous colours, which are odourless, while on the other hand many very inconspicuous flowers possess a strong odour. To the former group belong, e.g., the conspicuously coloured poppies (*Papaver Rhoeas*, *dubium*, *somniferum*, *Argemone*), *Glaucium*, *Chelidonium*, *Adonis aestivalis* and *autumnalis*, *Camellia japonica*, *Azalea*

indica, Centaurea Cyanus; and to the latter Vitis vinifera, Reseda odorata, &c. On the other hand, cases are not rare in which bright colouring is associated with strong odour, as in many roses, syringas, pinks, stocks, and generally in many cultivated plants that for this very reason are grown in gardens.

Delpino in 1873 ('Ult. oss.,' Atti Soc. ital. sc. nat., Milano, xvi, 1874) attempted a *Classification of the odours of flowers*. He distinguished two great groups, the *Sympathic* and the *Idiopathic*, which he arranged in five classes according to the following scheme:—

Classes of					
Sympathic.		Idiopathic.			
$\frac{5}{6}$	$\frac{1}{6}$	Sweet	odours
$\frac{4}{6}$	$\frac{2}{6}$	Aromatic	"
$\frac{3}{6}$	$\frac{3}{6}$	Fruity	"
$\frac{2}{6}$	$\frac{4}{6}$	Unpleasant	"
$\frac{1}{6}$	$\frac{5}{6}$	Nauseous	"
				} Sympathic Odours.	
				} Idiopathic Odours.	

Delpino describes as *sympathic* odours, those that are more or less agreeable to a large number of insects (bees, wasps, flies, beetles) and also to man. He applies the term *idiopathic* to odours that are sympathetic to only a few animals, but that on the contrary are antipathic to a large number.

A. SYMPATHIC ODOURS (Odori simpatici).

Class I: Sweet Odours (Odori suavi).

1. *Jessamine-odour* (Odore gelsominaceo): Jasminum grandiflorum, sp. of Gardenia, Heliotropium europaeum, Coffea arabica, Solanum bonariense, Passiflora quadrangularis, and others.

2. *Narcissus-odour* (Odore narcissino): Narcissus Jonquilla, viridiflorus, Tazetta, and others; Ornithogalum longibracteatum, Reseda alba, Hemerocallis flava, Heliotropium grandiflorum, and others.

3. *Mignonette-odour* (Odore resedino): Reseda odorata, and others.

4. *Hyacinth-odour* (Odore giacintino): Hyacinthus orientalis, Lunaria rediviva.

5. *Lily-odour* (Odore liliaceo): Lilium candidum, Convallaria majalis, Asperula odorata, Crinum asiaticum and other species, Lonicera Caprifolium.

6. *Nuphar-odour* (Odore nufarino): Nuphar luteum, Phoenix dactylifera, ? Nymphaea alba.

7. *Spartium-odour* (Odore spartino): Spartium junceum, Vanda insignis.

8. *Violet-odour* (Odore violaceo): Viola odorata, Rondeletia odorata, Cheiranthus Cheiri.

9. *Honey-and-wax-odour* (Odore melleo e cereo): Symphytum officinale, tuberosum, orientale; sp. of Acer, Galium verum, Herminium Monorchis, Haematoxylon campechianum, Apocynum adrosaemifolium.

10. *Hawthorn-odour* (Odore crategino): Crataegus oxyacantha, Sorbus Aucuparia, Ornithogalum arabicum, Allium neapolitanum, sp. of Spiraea, Cimicifuga racemosa, Cornus sanguinea, Ailanthus glandulosa, Sisymbrium pinnatifidum, Tamarix

tetrandra, *Smilax aspera*, *Ligustrum vulgare*, *Orchis coriophora*, *Prunus domestica*, *lusitanica*, *Amygdalus communis*.

11. *Ambrosial* or *rose-odour* (Odore ambrosiaco o di rosa): *Rosa moschata*, *arvensis*, *pumila*, *sempervirens*; *Sanguisorba dodecandra*, *Paeonia Moutan*.

12. *Balsam-odour* (Odore balsamico): *Gladiolus viperatus*.

13. *Hay-odour* (Odore di fieno o benzoico?): *Dracaena fragrans*, *Heliotropium indicum*, *Asperula taurina*.

14. *Orange* or *Lemon-odour* (Odore citrino o di limone): *Citrus medica*, *aurantiacum*; *Philadelphus coronarius*, *Cinchona magnifolia*, *Magnolia grandiflora*, *Cereus strigosus*, *Iris aphylla*.

15. *Musk-odour* (Odore moscato): *Hoya viridiflora*, *Allium moschatum*, *Solanum nigrum* and *villosum*, *Physalis Alkekengi*.

16. *Acacia-odour* (Odore acacino): *Acacia Farnesiana*.

17. *Coryanthes-odour* (Odore coriantino): *Coryanthes macrantha*, *Stanhopea grandiflora*, *Gloxinia maculata*.

Class II: Aromatic Odours (Odori aromatici).

18. *Carnation-odour* (Odore cariofillino): *Dianthus Caryophyllus*, *plumarius*, *monspessulanus*; *Petasites vulgaris*, *Gladiolus tristis*, *Alstroemeria caryophyllea*.

19. *Vanilla-odour* (Odore vaniglino): *Heliotropium peruvianum*, *Petasites fragrans*, *Erica fragrans*, *Cereus grandiflorus*, *Epipactis microphylla*, *Spiranthes autumnalis*, *Nigritella angustifolia*, sp. of *Selenipedium*, *Phyteuma spicatum* (?).

20. *Cinnamon-odour* (Odore cinnamomeo): *Maxillaria aromatica*, *Rosa cinnamomea*.

21. *Nutmeg-odour* (Odore miristicino): *Anonaceae*.

22. *Laurel-odour* (Odore laurino): *Ilicium religiosum*.

Class III: Fruity Odours (Odori carpologici).

23. *Banana-odour* (Odore musaceo o di banano): *Magnolia fuscata*, *Calycanthus floridus*, *Anona tripetala*, *Rochea coccinea*.

24. *Apricot-odour* (Odore armeniaco): *Plumeria alba*, and others.

25. *Pineapple-odour* (Odore ananasino): *Victoria regia*, sp. of *Calycanthus*, *Colocasia odora*.

26. *Turnip-odour* (Odore rapaceo): *Cereus Napoleonis*.

B. IDIOPATHIC ODOURS (Odori idiopatici).

Class IV: Unpleasant Odours (Odori graveolenti).

27. *Elder-odour* (Odore sambucino): *Sambucus nigra*, *Orchis sambucina* (?), *Thalictrum aquilegifolium*.

28. *Goat-odour* (Odore ircino o spermatico): Sp. of *Elaeagnus*, *Valeriana officinalis*, *Kakosmanthus macrophyllus*, *Himantoglossum hircinum*, *Cypripedium villosum* and *purpuratum*.

29. *Bug-odour* (Odore cimicino): *Rosa Eglanteria* and *laxa*, *Delphinium speciosum* and *triste*, *Orchis coriophora*.

30. *Beetle-odour* (Odore scarabico): *Cornus paniculata*, *Crataegus Oxyacantha*, *Sorbus Aucuparia*.
 31. *Bitumen-odour* (Odore bituminoso): *Iris viscaria*.
 32. *Onion-odour* (Odore alliaceo): *Pothos foetida*.
 33. *Rue-odour* (Odore rutaceo): *Aristolochia Bonplandi*.
 34. *Poppy-odour* (Odore readino): *Papaver Rhoeas*, *Aristolochia trilobata*.
 35. *Tobacco-odour* (Odore tabacino): *Aristolochia gigas*.
 36. *Rhodea-odour* (Odore rodeino): *Rhodea japonica*.
 37. *Pea-odour* (Odore pisino): *Gonolobus hispidus*.
 38. *Fig-odour* (Odore sicioides): *Ferraria undulata*.
 39. *Fermentation-odour* (Odore zimotico): *Asimina triloba*.

Class V: Nauseous Odours (Odori nauseosi).

40. *Putrid-odour* (Odori di lezzo): *Arisarum vulgare*, *Euonymus verrucosus*, *Cynanchum nigrum*.
 41. *Putrid fish-odour* (Odore saprietino): *Aristolochia labiosa*.
 42. *Urine-odour* (Odore urinoso): *Arum italicum*, *maculatum*; *Aristolochia Siph.*
 43. *Excrement-odour* (Odore stercoreo): *Hibbertia volubilis*, *Carica digitata*, *Brachystelma tuberosum* and *crispum*.
 44. *Mephitic* or *viverrine-odour* (Odore mefitico o viverrino): *Symplocarpus foetidus*.
 45. *Corpse-odour* (Odore cadaverino): *Arum Dracunculus*, *crinitum*, *trilobatum*; *Aristolochia grandiflora*, *foetens* (?); *Stapelia grandiflora*, *hirsuta*, *variegata*, and others; *Rafflesia Arnoldi*, *Brugmansia Zippelii* (?), sp. of *Saprina*, *Hydnora africana*, *Sapranthus nicaraguensis*.

Kerner has also attempted ('Nat. Hist. Pl.,' Eng. Ed. I, II, pp. 199-203) to classify odours, the number of which he estimates as being at least 500. He distinguishes five groups of floral odours.

1. Indoloid Odours. To this group belong odours that arise during the decomposition of albuminoid substances. It therefore includes odoriferous bodies of nitrogenous nature, and containing one or several benzol nuclei, e.g. skatol and indol, which both appear as constant constituents of human faeces and give these their specific odour. Such odours of dung, decomposing urine, putrefying flesh, stinking fish, &c., are found in numerous Aroideae (*Arum maculatum*, *Arisarum vulgare*, sp. of *Amorphophallus*, *Dracontium*, *Stauromatum*, *Arisaema*, and others), *Asclepiadaceae* (*Stapelia*), *Balanophoreae*, *Hydnoreae*, *Anonaceae* (*Asimina triloba*, *Sapranthus nicaraguensis*, *Uvaria grandiflora*), many *Aristolochiaceae* (*Aristolochia Gigas*, *grandiflora*, *foetens*, sp. of *Bragantia*, *Thottea*, *Lobia*), and *Rafflesiaceae* (*Rafflesia*, *Brugmansia*, *Saprina*, *Hydnora*). Flowers with an indoloid odour frequently possess a dull brown, dark violet, black purple, spotted, or flesh and blood colour, which along with the putrescent smell attracts carrion-loving flies.

2. Aminoid Odours. To this group Kerner assigns all those odoriferous substances that have as foundation primary, secondary, or tertiary amines, i. e. bodies

that are regarded as having been derived from ammonia, hydrogen atoms of this being replaced by an alcohol radical. The best known odour belonging to this group is that of the hawthorn (*Crataegus Oxyacantha* and *monogyna*) which suggests the smell of herring brine, and is due to trimethylamine. As Kerner mentions, the odour of hawthorn is found with slight variations in the flowers of the pear (*Pyrus communis*), medlar (*Mespilus germanica*), rowan (*Sorbus Aucuparia*), many meadow-sweets (e.g. *Spiraea ulmifolia*, *chamaedryfolia*), guelder-rose and way-faring-tree (*Viburnum Opulus* and *Lantana*), chestnut (*Castanea vesca*), racemose elder (*Sambucus racemosa*), wild clematis (*Clematis vitalba*), and barberry (*Berberis vulgaris*). Similar also is the odour of horse-chestnut (*Aesculus Hippocastanum*), manna-ash (*Fraxinus Ornus*), ivy (*Hedera Helix*), and others. I may here at once point out a peculiarity that is common to most of the flowers just mentioned, i.e. that they conceal their honey very superficially, so that it is accessible to insects with the shortest proboscis. In fact such insects, especially flies (*Muscidae*), are particularly conspicuous as visitors of these flowers.

3. Benzoloid Odours. These are odours that are peculiar to the derivatives of benzol, in which the hydrogen atoms of a benzol nucleus are replaced by alcohol or acid radicals. Kerner assigns to this group the odour, due to engenol, of several carnations (*Dianthus Caryophyllus*, *plumarius*, *superbus*), also the odour of hyacinths (derived from cinnamyl-alcohol), the odour of *Spiraea Ulmaria* (derived from salicyl aldehyde), the cumarin-odour of woodruff, and the vanilla-odour of heliotrope; and beside these the respective odours of lilac (*Syringa vulgaris*), lily of the valley (*Convallaria majalis*), mignonette (*Reseda odorata*), jessamine (*Jasminum officinale*), auricula (*Primula Auricula*), honeysuckle (*Lonicera Caprifolium*), false acacia (*Robinia Pseudacacia*), violet (*Viola odorata*), sow-bread (*Cyclamen europaeum*), Paulownia (*P. imperialis*), and Ylang-ylang (*Unona odoratissima*), to which may be added the plum-like odour of *Muscari racemosum* and *Polygala Chamaebuxus*.

The varieties of benzoloid odour just named are repeated, with some modification, in many other flowers, a number of which are given by Kerner. The following possess:—

(a) *Carnation-odour*: *Orobanche caryophyllacea*, *gracilis*, *lucorum*; *Platanthera bifolia*, *Gymnadenia conopsea*, *Ribes aureum*, *Narcissus poeticus*;

(b) *Hyacinth-odour*: *Silene nutans*, *longiflora*, *noctiflora*; *Hesperis tristis*; *Pelargonium atrum*, *glaucofolium*, and others;

(c) *Woodruff-odour*: *Anthoxanthum odoratum*, *Hierochloa odorata*, species of *Melilotus* (mixed in these last with the odour of honey);

(d) *Vanilla-odour*: *Heliotropium peruvianum* and *europaeum*; *Asperula glomerata*, *cynanchica*, *longiflora*; *Linnaea borealis*, *Sambucus Ebulus*, *Convolvulus arvensis*, *Gymnadenia odoratissima*, *Nigritella nigra*, *Saussurea alpina*, *Daphne alpina*, *Epipogon aphyllum*;

(e) *Lilac-odour*: *Daphne striata* and *pontica*.

(f) *Lily-of-the-Valley-odour*: *Echinocactus Tetani*;

(g) *Acacia-odour*: *Cytisus alpinus*, *Spartium junceum*, *Iris odoratissima*;

(h) *Auricula-odour*: Sp. of *Primula*, *Trollius europaeus*;

(i) *Honeysuckle-odour*: *Nicotiana affinis*;

(k) *Violet-odour*: *Viola mirabilis*; *Matthiola annua*, *incana*, *varia*; *Cheiranthus Cheiri*, *Hesperis matronalis*, *Leucojum vernum*, *Gentiana ciliata*, *Daphne Laureola*, *Nymphaea coerulea*, *Sarracenia purpurea*;

(l) *Cyclamen-odour*: *Pyrola uniflora*;

(m) *Paulownia-odour*: *Glycine chinensis*;

(n) *Ylang-ylang-odour*: *Zaluzianskia lychnidea*.

The above-named flowers with odours agreeable to man all conceal their honey much more deeply than the flowers of the former group, so that it is only accessible to insects possessing a moderately long or very long proboscis. Accordingly, the benzoloid odours are agreeable to those insects (bees, moths, and butterflies) which are the most industrious floral visitors.

4. Paraffin Odours. Among these Kerner includes odours that are peculiar to those acids and alcohols among hydrocarbons described as paraffins. Special forms of them are the valerian odour of *Valeriana officinalis*, *montana*, and *saxatilis* (due to valerianic acid); the rose-odour (due to pelargonic acid), especially characteristic of *Rosa centifolia*; the rue-odour of *Ruta graveolens* (due to oil of rue); the vine-flower-odour (due to aenanthic acid) of *Vitis vinifera*, *Gleditschia triacanthos*, and *G. sinensis*; the linden-odour of *Tilia alba*, *parvifolia*, and others; and *Aesculus macrostachya*; the nightshade-odour of *Datura Stramonium*, and others; *Mandragora*, *Petunia*, and *Paonia*; the elder-odour of *Sambucus nigra* and *Orchis pallens*; and the goat-odour (due to caproic acid) of *Himantoglossum hircinum* and *Orchis pallens*.

Kerner's 'paraffinoid' odours seem to me to constitute the least consistent group. The disagreeable odour of rue, of *Datura*, and of valerian is in such sharp contrast to the delightful fragrance of the vine and rose that I cannot regard the paraffinoid odours as a natural group, in spite of their chemical affinity. Moreover, the circle of visitors of the flowers concerned is heterogeneous, including flies and bees, insects which respectively possess the shortest and the longest proboscides and are the idlest and busiest guests.

Kerner is doubtful whether the *odour of honey* should be classified here, for it is not due, as formerly supposed, to myricil alcohol (a paraffin derivative). The odour of honey is the commonest of all the odours of flowers. It occurs, according to Kerner, in many natural orders, e.g. in the flowers of the sloe (*Prunus spinosa*), apricot (*P. Armeniaca*), cherry (*P. avium*), almond (*Amygdalus communis*), *Hermium monorchis*, *Prunus Padus* (combined with an aminoid odour, according to my experience), *Galium cruciata*, *vernum*, *verum* (combined with odour of woodruff, in my opinion), *Myosotis alpestris*, *Phlox paniculata*, *Asclepias*, *Cynanchum*, *Corydalis cava*, *Euphorbia Cyparissias*, *Salix Caprea*, *daphnoides*, and others; *Cirsium arvense*, *Angelica officinalis*, *Heracleum Sphondylium*, *Meum Mutellina*, *Pimpinella magna*, *Alyssum montanum*, *Erysimum odoratum*, *Tulipa sylvestris*, *Allium sibiricum*, *Chamaemoly*, and others; *Polygonum Fagopyrum*, *Trifolium pratense*, *resupinatum*, *Lathyrus odoratus*, and others.

5. Turpenoid Odours. These are such odours as are derived from terpenes, i.e. ethereal oils which do not contain oxygen. These are sometimes enclosed in special cells within the plant-body, sometimes in stalked epidermal glands on the stem or leaves, more rarely on the flowers. Oil of neroli, for instance, produces

the odour of orange-flowers, which also occurs in the flowers of species of *Citrus*, and in a few species of *Magnolia*. The citron-odour of *Thymus citriodorus*, *Th. montanus* and *Dictamnus* is due to citron-oil contained in the flowers, that of *Lavendula* to the oil of lavender.

Kerner's classification of odours is a very praiseworthy constructive effort, as here, for the first time, grouping has been attempted on a *scientific* foundation, according to the chemical composition of the odoriferous substances. That it is only an attempt Kerner himself emphasizes. There is great difficulty in determining the odours of flowers, more especially because it is largely a subjective matter: as Kerner remarks—one observer thinks he recognizes the odour of vanilla where another perceives that of the violet. Both may be right, because, as a matter of fact, two kinds of odour may simultaneously emanate from the same flower. But it must be added that the sense of smell is very liable to be deceived; while taste and sight may both be concerned with such illusion (Kerner, *op. cit.*, p. 203). When we see a carnation, the odour of carnations at once comes to mind. This may happen before the odour proceeding from the carnation reaches the organs of smell. It is therefore recommended that in determining an odour the flower should not be looked at at all, the investigation being made with closed eyes.

Odours agreeable to bees, lepidoptera, and hover-flies are also, as a rule, acceptable to man, while many (e.g. indoloid and aminoid odours) which are pleasing to flies are disagreeable to human beings. Carrion-flies and dung-flies in particular (*Sarcophaga*, *Calliphora*, *Scatophaga*, *Lucilia*, and others) take pleasure even in odours that are disgusting to us, licking and probing products of decomposition (dunghills, decomposing flesh, liquid manure, pus, carrion) the colour and smell of which fill us with loathing. There are also certain small flies and gnats, especially moth-flies (*Psychodidae*), which are everywhere common in closets, and delight in the above-named disgusting substances. All these insects prefer to visit flowers possessing odours or colours repulsive to us, and which have therefore already been described (see p. 67) as *Nauseous Flowers*. Kerner (*op. cit.*, p. 206) also advances the view that many odours which are not perceived by man, are perceptible to certain insects. As already mentioned (see p. 87), Kerner explains the regular visits of *Andrena florea* to the small greenish flowers of *Bryonia dioica*, which, though half hidden among foliage, it knows how to find, by supposing the existence of an odour which is only perceived by this particular bee. The flowers are practically odourless to human beings. The inconspicuous green flowers of *Ampelopsis quinquefolia*, scentless to us, are visited by bees, according to Kerner, with great eagerness and industry. These insects may be seen flying to the plant from all sides in a way leaving no doubt that its flowers are recognized at a considerable distance. 'As it is not sight, it must certainly be the smell that leads to this recognition. The flowers are odourless to human beings.' Kerner (*op. cit.*) gives the following additional examples of inconspicuous flowers, which, though apparently scentless to man and many animals, are eagerly sought out by particular insects—*Aristolochia Clematitis*, *Vaccinium Myrtillus*, *Chamaeorchis alpina*, and *Listera ovata*. Kerner also thinks that the characteristic odour of many brightly coloured flowers explains the constancy with which certain insects visit the same species more or less exclusively. According to Kerner's view the odours of such flowers

are only perceived by these special visitors, or are at any rate peculiarly sympathetic to them. For example—

Andrena florea *F.* is found exclusively in *Bryonia dioica* *Jacq.* (vide supra);
Andrena Hattorfiana *F.* and *Cetii* exclusively on *Knautia arvensis* *Coult.* ;
Andrena Nasuta *Gir.* exclusively on *Anchusa officinalis* *L.* ;
Bombus Gerstaeckeri *Mor.* exclusively on *Aconitum Lycoctonum* *L.* ;
Cilissa melanura *Nyl.* almost exclusively on *Lythrum Salicaria* *L.* ;
Macropis labiata *Pz.* almost exclusively on *Lysimachia vulgaris* *L.* ;
Osmia adunca *Latr.* and *Caementaria Gerst.* almost exclusively on *Echium*.

On the other hand, bees of the genus *Prosopis*, which themselves possess a strong odour, prefer to seek out flowers that have a powerful smell, due to their containing ethereal oils—e.g. *Ruta*, *Anethum*, *Reseda*, *Lepidium*, *Achillea*, *Matricaria*.

Many flowers are almost entirely scentless during the day, and exhale a very strong odour in the evening and at night. These are, without exception, *moth flowers* (see p. 67).

Flowers offer **Pollen**, and usually also **Nectar** or enclosed **Sap**, as food to the insects that have been enticed by colour or odour ; and in return for this the visitors, as a rule, effect transference of pollen, cross-pollination being thus brought about in many cases. Sometimes flowers also afford insects **Shelter**, which they can leave again at pleasure, or else they are compelled to make an unwilling stay of considerable duration.

Pollen alone, as a reward for work done, is offered by relatively few flowers to the insects that visit them and thereby effect pollination. These *Pollen Flowers* will be considered more fully later on (cf. p. 105).

Secretion of Nectar usually takes place deep down in the flower by means

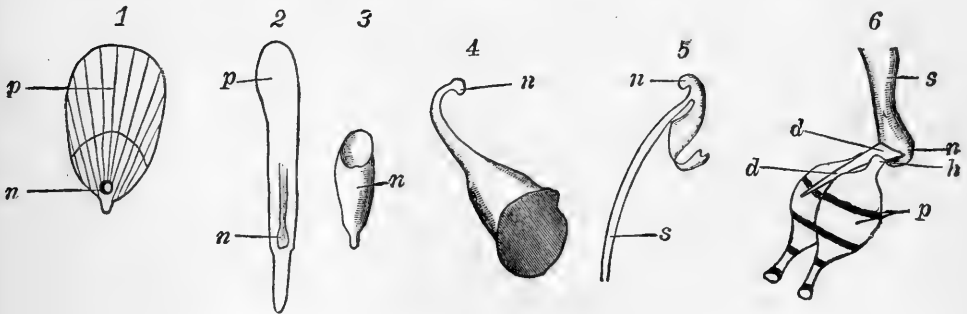


FIG. 12. Nectaries of some Ranunculaceae. (Enlarged. From Nature.)

1. *Ranunculus sceleratus*, *L.*

2. *Trollius europaeus*, *L.*

3. *Helleborus niger*, *L.*

4. *Aquilegia vulgaris*, *L.*

5. *Aconitum Napellus*, *L.*

6. *Nigella arvensis*, *L.*

n, Nectary.

p, limb.

s, stalk.

d, cover.

h, protuberance.

of special glands (nectaries). These are sheltered in the most varied ways : between a fully-exposed position, e.g. in most of the Umbelliferae, and concealment in long corolla-tubes (*Lonicera Caprifolium*), or in long spurs (*Corydalis cava*), there are numerous gradations, so that Herm. Müller has established eight classes of flowers, according to the position of the nectar, and the insect visits which are determined by

this. These will be thoroughly described later on (cf. also p. 67). In this place the various forms of nectary will not be fully considered, but one example may serve to indicate in what variety these organs may occur even within a single family, the Ranunculaceae (Fig. 12).

The form of the nectaries is not always the same, even in one and the same species of plant. Herm. Müller gives in his works two particularly striking examples of the kind, i.e. *Ranunculus auricomus* ('Fertilisation,' p. 79) and *R. pyrenaicus* ('Alpenblumen,' p. 133) (see Fig. 13).

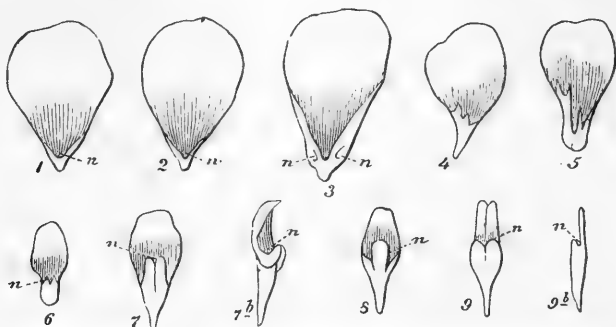


FIG. 13. (1-8) Different petals of *Ranunculus auricomus* with diversely-formed nectaries (n).
(9) Petal of *Eranthis hyemalis*. (After Herm. Müller.)

Nectar-covers, which also were frequently mentioned by Sprengel, and which are formed by projecting parts of flowers, processes, hairs, and so forth, serve as a means of protecting nectar from rain. Owing to such shelter nectar is not only saved from dilution, or even from being washed away, but more abundant secretion and accumulation are also rendered possible, with the result that insect visits are more numerous. On the other hand, since the nectar is sheltered deeper down, numerous of the less industrious insects are debarred from visiting and pollinating the flowers.

In order to render more easy the finding of nectar by insects that have been attracted by colour or odour there are, as Sprengel pointed out (see pp. 4-6), many spots or lines on the flower, which by their position or direction indicate the place where the honey is concealed (cf. Fig. 14). These **Nectar-guides**, however, are naturally only present in such flowers as are visited by insects during the day. They are wanting (see p. 67) in moth flowers, where they would be useless (cf. also Sprengel, 'Entd. Geh.,' p. 16).

The nectar-guides of one and the same species of plant have not always the same form, but may be developed in various ways. I have described ('Bl. u. Ins. a. d. Nordfries. Ins.,' p. 52) and figured (see Fig. 15) such variable nectar-guides in *Erodium Cicutarium*.

The correctness of Sprengel's theory of nectar-guides has often been doubted; but it may be accepted as valid till some other and better explanation can be given of the dots, lines, streaks, and markings that occur on the petals of flowers.

In support of Sprengel's theory of nectar-guides Hildebrand mentions ('Die Farben der Blüten,' p. 72) a phenomenon frequently exemplified by double flowers. It appears that when nectar-guides are strikingly developed in the simple form of

such flowers they disappear more or less completely in the double variety, where they have become mere useless markings. Insects are certainly attracted from a distance by these flowers, but as soon as they come near they notice that here there is nothing for them (for as a rule the formation of pollen and the secretion of nectar cease when flowers become double), and turn away without searching for food.

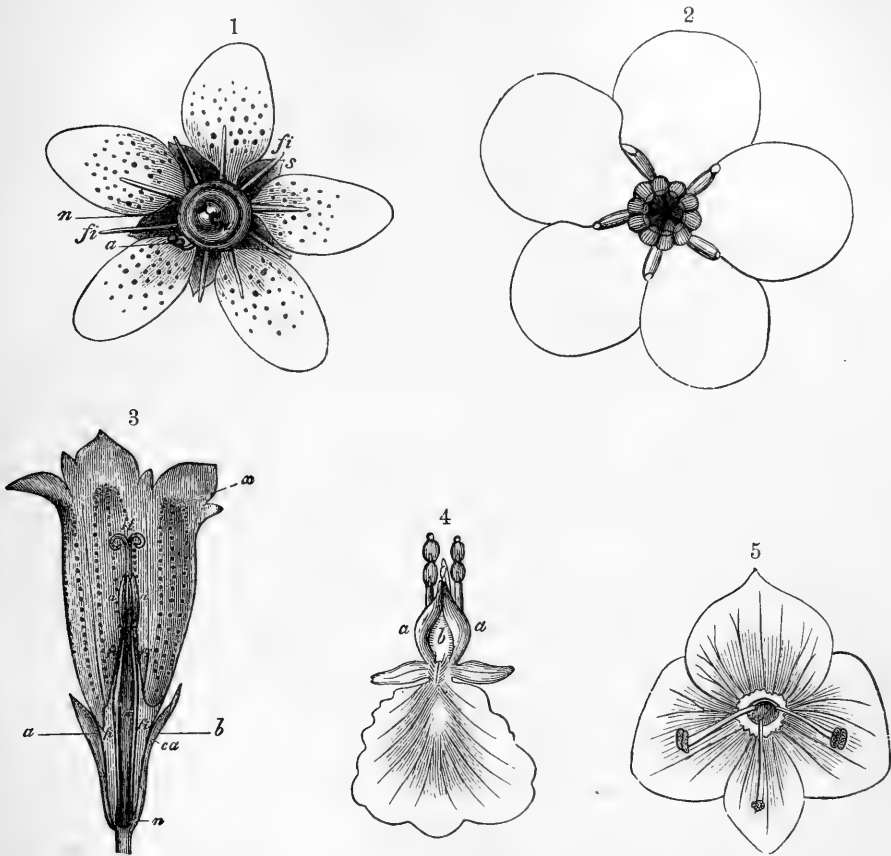


FIG. 14. *Nectar-guides*. (1) Dotted marks of *Saxifraga aspera* L. (2) Ring-shaped nectar-guide of *Myosotis alpestris* Schmidt. (3) Spots and streaks of *Gentiana acaulis* L. (4) Streaks on the lower lip of *Teucrium Chamaedrys* L. (5) Streaks and ring-shaped nectar-guide of *Veronica Chamaedrys*.

Delpino ('Ult. Oss., Atti Soc. ital. sc. nat.,' Milano, xvi, 1874, pp. 234 et seq.) distinguishes between *intra-floral* nectaries, occurring in the flower, and *circum-floral* nectaries on its outer side, as e.g., in *Euphorbia*, where the honey is secreted by crescentic or rounded appendages of the cup-shaped involucre. There may also be *extra-floral* nectaries outside the flower altogether, but situated near it, as in the case of the above-mentioned (pp. 73-4) *Marcgraviaceae*, which investigations of Thomas Belt ('The Naturalist in Nicaragua,' 1874) made known to us. In this family nectar is secreted by bracts of striking form and colour by which the humming-birds that effect pollination are attracted.

Besides these three kinds of nectaries occurring in the region of the flower, and

all serving to attract animals that effect pollination, so that they are described as *nuptial*, other nectaries are sometimes to be found on the vegetative organs of plants, which serve totally different purposes, and have at most but an indirect relation to the crossing of flowers. These organs, which are described by Delpino as *extra-nuptial*, by Kny as *asexual* nectaries, serve to allure ants, which afford protection to the plants against the attacks of other animals, and so form a kind of body-guard. Sprengel ('Entd. Geh.,' p. 356) noticed these extra-floral nectaries, and also the visits of ants

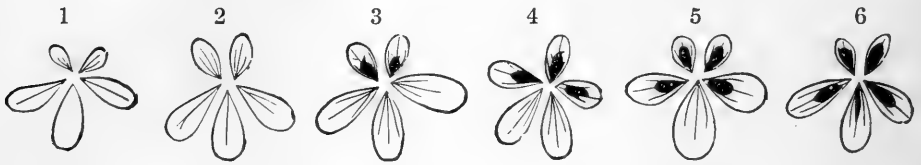


FIG. 15. *Various forms of Nectar-guides in Erodium Cicutarium.* (From Nature.) (1) The two upper petals are relatively shorter, broader, and coloured a darker red, with two or three dark veins; the two lower lateral ones are relatively longer, narrower, and coloured brighter red, with a dark mid-rib; the fifth petal (the middle of the three lower) is the longest, narrowest, brightest, and is veinless. (2) The two upper petals have each three long veins; on each of the two lateral lower petals there are one or two somewhat branched lines; the fifth (middle lower) has a central vein. (3) The two upper petals have three veins that are in part branched and possess a dark basal spot; the three lower have each three veins. (4) Three petals have three partially-branched veins and a dark basal spot (largest in the middle one); two petals have each only three veins. (5) The two upper petals have each three branched veins and a large dark basal spot; of the three lower petals the two lateral ones have each three veins and a smaller dark spot; the middle one has three veins. (6) The two upper petals have a spot that covers almost the entire surface, as well as the three veins; the two lateral of the lower petals have three veins, and a medium-sized spot, the middle lower petal has also three veins and a somewhat smaller spot. (Cf. Knuth, 'Blumen und Insekten auf den nordfriesischen Inseln,' p. 52.)

to *Vicia sepium*: 'This plant provides nectar for insects not only in its flowers but also on its stipules. These have on their under side a small cavity, which is not of so dark a green as the leaves, but is slightly yellowish and contains a drop of nectar. The great wood-ants search eagerly for this fluid.' The significance of the extra-floral nectaries as secretory organs serving to attract protective ants was first recognized by Delpino (1873): but his investigations are outside the actual limits of flower pollination, and so are only referred to here.

According to what has been just stated, nectaries may be classified as—

i. **Nuptial:**

1. Intra-floral.
2. Circum-floral.
3. Extra-floral.

ii. **Extra-Nuptial.**

Even in pollen flowers a marking like a nectar-guide is sometimes found on the petals, and this has been described as a pollen-guide. This term does not seem to me to be correct, for the mark always points to the place where nectar should occur, not to where pollen is found. I would therefore propose the term *pseudo-nectar-guide*. The erect yellow standard of the pollen flower *Ononis natrix*, for example, possesses red streaks running towards the base of the flower.

Sap. As Sprengel ('Entd. Geh.,' p. 3) long ago pointed out, *Orchis latifolia* and *O. Morio* have the typical structure of nectar flowers, but contain no nectar.

Sprengel described such forms as 'false nectar flowers.' The observations of Charles Darwin and Herm. Müller have proved that the visitors bore into the juicy cellular tissue of our species of Orchis, and thus procure nourishment. Müller has also shown that very probably some visitors of *Cytisus Laburnum* and *Erythraea Centaurium* bore for sap that is enclosed in the flowers, and it is not improbable that the more industrious bees and *Lepidoptera* may pierce many other flowers for the same purpose, using the tip of their proboscis as a boring-instrument. It is a fact that *Lepidoptera*, which are only able to feed on fluids, not infrequently remain for a considerable time on pollen flowers with the proboscis sunk in their bases, e.g. *Helianthemum alpinum* (Herm. Müller, 'Alpenblumen,' p. 162), so that we are justified in assuming that these insects bore for sugary juice. In other plants, e.g. in species of *Pinguicula*, instead of nectar the visitors find little knobs distended with sap, that seem to offer them nourishment. In species of *Verbascum*, *Hypericum*, and *Lysimachia*, club-shaped glandular hairs on the filaments, or similar hairs on the inner side of the petals, appear to supply material for moistening the pollen, and causing it to stick. Such peculiarities of particular flowers will be dealt with at length in the second volume of this work.

Besides pollen, nectar, and juices obtained by boring or gnawing, many insects take from the flowers they visit other parts not originally destined for this purpose. Numerous flower-visiting beetles (*Chrysomelidae*, *Lamellicornia*, *Curculionidae*) devour stamens, petals, or other floral parts, and thus inflict almost unmixed injury, since they only exceptionally confer the benefit of cross-pollination. In individual

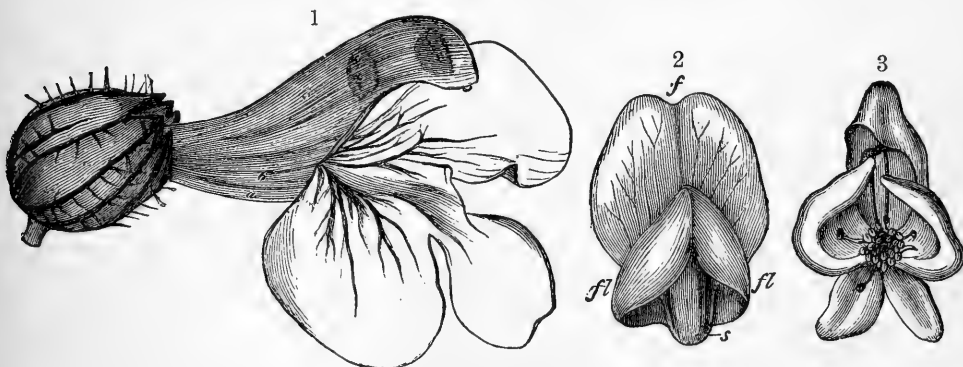


FIG. 16. *Alighting-Places.* (1) *Pedicularis verticillata*, L.; the lower lip serves as an alighting place. (2) *Hippocrepis comosa*, L.; the wings and keel are alighting-places. (3) *Aconitum Napellus*, L.; the two lower sepals serve as platforms.

cases, however, the damage may be compensated for by the benefit (e.g. in *Crambe maritima*, see p. 102), or, the destroyers of certain floral parts may even be absolutely indispensable for the pollination of the plant (cf. *Yucca* and *Ficus*, pp. 102-4).

The visits of insects effecting the pollination of flowers may be facilitated by the provision of a **seat**, which is as comfortable as possible. Such small flowers as are united into conspicuous societies have suitable resting-places in their crowded inflorescences. The capitula of the *Compositae*, the umbels of the *Umbelliferae*, the catkins of willows, and the like, are at the same time both chair and spread table. Larger flowers frequently possess special alighting-places, e.g. the *Leguminosae* in

their wings and keel, the Labiatae and Scrophulariaceae in their lower lip, and similarly in Orchids, many Ranunculaceae, and so on (cf. Fig. 16). The special arrangements of this kind will be dealt with in the second part of this work in connection with the description of particular floral adaptations. The alighting place is always so situated that insects suitable for the work of pollination touch either the pollen-covered anthers or the receptive stigma. On the other hand, such insects as are not able to effect pollination, and are therefore useless or even in many cases injurious to the plant, are kept away from the flower by very varied contrivances. Kerner, who has described such insects as Unbidden Guests, distinguishes the following **Protective Arrangements** ('Nat. Hist. Pl.,' Eng. Ed. 1, II, pp. 231-43):—

1. Against wingless animals that creep up from the ground.

(a) *The nectar of extra-floral nectaries keeps ants away from the flowers*—as these insects make use of the honey thus found on the way up, and do not trouble to go to the flowers: *Impatiens tricornis*.

(b) *Isolation of the plants by water*. Owing to the habitat of the plants being in water, their flowers are only accessible to flying insects; the blossoms of all marsh- and water-plants are thus protected against creeping animals. The water collecting in the leaf-sheaths of *Dipsacus* and *Silphium perfoliatum*, and in the funnel-shaped sheaths of the leaf-rosettes in many Bromeliaceae (*Aechmea*, *Tillandsia*, *Billbergia*, *Lamprococcus*), serves the same purpose.

(c) *Access to the flowers prevented by sticky material*, occurring either as rings or streaks on the stem (e.g. in *Silene Otites*, *Viscaria vulgaris*), or else in the form of adhesive glands or glandular hairs on the peduncles and calyces (e.g. *Ribes Grossularia*, *Epimedium alpinum*, *Circaea alpina*), or on the foliage leaves (*Pinguicula vulgaris* and species of *Drosera*, in which the visitors are afterwards digested by the leaves).

(d) *Hindrance by wax-like coatings on the peduncles and twigs*. The slipperiness thus produced interferes with access to the flowers, e.g. in *Salix daphnoides* and *S. pruinos*.

(e) *Sharp thorns, prickles, or stiff bristles on stems, leaves, or inflorescences* prevent soft-skinned creeping animals, especially snails and slugs, from climbing up to the flowers (*Ulex*, *Rubus*, *Eryngium*, and many others).

2. Against unbidden guests which can fly.

(a) *By the development of hairs and bristles inside the flower*, which either completely fill it, or only make up a hirsute circlet or tuft above the nectary. Weels and gratings are thus constituted, which prevent small unbidden guests from entering the flower, while an invited one is able to thrust its proboscis between the bristles (*Veronica officinalis*, *Lonicera alpigena*, *Menyanthes trifoliata*, and others).

(b) *By the development of special floral arrangements*, which can only be opened by insects that are specially adapted for the work of pollination, as in numerous Papilionaceae, Labiatae, Scrophulariaceae, *Corydalis cava*, and others.

(c) *By an inflated vesicular calyx*, which serves to protect the flowers, especially against honey-stealing humble-bees. There are two humble-bees in particular which in consequence of the shortness of their proboscis are not able to reach in the usual

way the nectar of numerous flowers, though it is easily got at by related species possessing a longer proboscis. They are *Bombus terrester* L., and *Bombus mastrucatus* Gerst., which is very common in the Alps. These forms, by biting through the nectar-containing organs from the outside, and introducing their proboscis into the opening so made, steal the nectar, and are therefore not only useless to the plant, but are frequently injurious. We may regard the inflated calyx of, e.g. *Silene inflata*, as a protection against such nectar-thieves, for it is so far away from the inner floral parts that they are not injured by the bites of these robbers.

(d) *By temporary cessation of allurements.* Flowers adapted to pollination by nocturnal Lepidoptera are almost or entirely odourless by day, and frequently look withered, while in the evening a stronger odour diffuses from them, and their petals and stamens are fully expanded: *Melandryum album*, *Silene nutans*, *Lonicera Periclymenum* and *Caprifolium*, *Hesperis tristis*, *Pelargonium atratum* and *triste*.

(e) *By ant-guards.* The nectaries already mentioned on p. 98, and which entice ants, also occur on the involucre bracts of the heads of some Compositae. The ants frequenting these heads in quest of nectar form a body-guard against beetles that eat the flower-buds, especially cockchafers and rosechafers (*Cetoniae*). Observations of the kind have been made on the capitula of several composites indigenous to South Europe, especially on *Centaurea alpina* and *ruthenica*, *Jurinea mollis* and *Serratula lycopifolia*. 'If one of the voracious beetles in question approaches, the ants immediately assume a defensive attitude, holding on firmly to the involucre bracts with the last pair of legs, and stretching the abdomen, the fore-legs, and especially their powerful jaws, towards the enemy. They remain in this posture, squirting out formic acid if necessary, till the marauder retreats; and not till this takes place do they once more peacefully turn their attention to the nectar' (Kerner, 'Nat. Hist. Pl.,' Eng. Ed. 1, p. 243). On the capitulum of *Jurinea mollis* there are often ten to fifteen ants of the species *Camponotus Aethiops*, and as many individuals of *Formica exsecta* have been observed on that of *Serratula lycopifolia*. When the capitula open, the beetles no longer settle upon the flowers, and the secretion of nectar ceases, so that the ants also abandon their visits.

Some flowers occasionally offer **Shelter** to their visitors, as well as pollen or nectar. During sudden rain, nectar-seeking or pollen-collecting guests eagerly take refuge under the overhanging upper lip of Labiates, in the flower-bells of species of *Campanula*, and within other flowers. Some of these even afford shelter for the night if the insects are overtaken by darkness while still at their work.

I have, for instance ('Bl. u. Ins. a. d. nordfr. Ins.,' p. 165), observed honey-bees making use of the upper lip of *Lamium album* as a shelter in rainy weather, and also now and again humble-bees in the flowers of *Campanula* *Trachelium* and other species, quite early in the morning, when the dew still lay on the plant, so that I was compelled to suppose that they had spent the night there. For the most part, however, it is smaller insects that seek shelter for the night in flowers or inflorescences, e.g. small bees belonging to the genera *Andrena*, *Halictus*, and *Panurgus*. The species of the first two of these stay overnight in the flowers of *Campanula* more particularly, while the species of *Panurgus* often spend the hours of darkness in the capitula of yellow-flowered composites (*Crepis*, *Hieracium*,

Hypochoeris, Taraxacum) belonging to the Cichoraceae, which they visit with special eagerness. Here they are protected by the marginal florets, which fold over them. Small beetles also, especially species of *Meligethes*, remain at night in the flowers or inflorescences they visit during the day, and in which, owing to the respiration of these floral parts, there is doubtless a higher temperature than in the surrounding air.

Even in the daytime the small flower-beetles just named often remain for many hours in one and the same flower, and may even stop there the whole day. Even larger beetles, such as the *Cetoniae*, linger a very long time in some flowers, especially in those of *Magnolias*, which Delpino for that reason has described as 'Käferblumen' (Beetle-flowers) (cf. p. 15). I have repeatedly observed the earwig (*Forficula auricularia*) staying for hours in flowers that are more or less closed, e. g. in those of *Tropaeolum majus*, *Trollius europaeus*, *Arisarum vulgare*, and others.

Sometimes the stay of insects in flowers or inflorescences is against their will. This is the case in 'pitfall-flowers,' such as *Arum maculatum*, *italicum*, and others. *Arisarum vulgare*, and *Aristolochia Clematitis*, in the flower-traps of which numerous small flies or moths are found; also *Dracunculus vulgaris*, in a single spathe of which Arcangeli found on one occasion 258 carrion-beetles. Insects enclosed in the flowers or inflorescences of pitfall-flowers are mostly compelled to stay in their recesses by hairs or bristles, which temporarily prevent egress until the anthers dehisce and the guests have covered themselves with pollen. Particulars with regard to these extremely remarkable flowers will be given in the sequel.

Flowers also now and then afford shelter to larval insects, which they allow to develop in their interior; as a return the adult insects effect pollination. In the flowers of *Crambe maritima*, for example, I observed numerous *Meligethes* larvae, which, like the beetles themselves, fed on the stamens and carpels. In spite of this they are not to be regarded as injurious to *Crambe*. For since the beetles are here the chief agents of pollination, if they and their larvae were present in smaller numbers many flowers would remain unfertilized, though it is also true that some would escape injury.

Still more interesting are the relations between *Yucca* and *Ficus*, and the moths or gall-wasps, respectively, which develop within their flowers. (See Fig. 17.)

Through the investigations and observations of W. Trelease, we know that the capsule-bearing species of *Yucca* indigenous to North America are pollinated by a moth, *Pronuba Yuccasella Trel.*, the females of which enter the flower that is open only at night, not in order to eat the pollen, but to carry it away, so as to provide their offspring with the necessary food. In order to render possible this transport of pollen, the first joint of the maxillary palp is very much elongated and can be rolled up, so that the *Yucca* moth can gather the pollen into a ball, which it holds under its head and carries away to another flower. Here the female clings to two filaments, introduces her ovipositor into the tissue of the pistil, and lays her eggs. She then pushes the pollen-ball that she has brought with her into the funnel-shaped stigma, so that pollination results. After a few days the larvae escape and are nourished by the young seeds, each of them consuming from eighteen to twenty before it is full grown. Pupation follows in the earth, after the larva has eaten through the wall of the ovary, and has let itself down by a thread which it spins. The seeds that are not consumed by the larvae then become ripe, and serve to propagate the species

of *Yucca* in question, while in the absence of the appropriate moth not a single seed would be set.

A relation between flowers and insects as remarkable as that presented by *Yucca* and its moth, obtains between the figs (*Ficus Carica* and others), and certain small



FIG. 17. *Transfer of pollen by egg-laying insects.* (1) A branch of the inflorescence of *Yucca Whipplei*; the flower in the middle is open, the one below it, which was open the previous day, is already closed, the other flowers are still in the condition of buds. (2) A single flower of the same plant visited by the moth *Pronuba Yuccasella*; the three anterior petals removed. (3) Stigma of *Yucca Whipplei*. (4) *Pronuba Yuccasella* flying to *Yucca Whipplei* in the moonlight. (5) Head of the insect, with its proboscis-like maxillary palps, holding fast a ball of pollen. (6) Branch of *Ficus pumila* with urn-shaped inflorescence divided longitudinally. (7) A single female flower from the base of this urn. (8), (9) Stamens from the upper part of the same. (10) Urn of *Ficus Carica* filled with galls produced by *Blastophaga*, and divided longitudinally; near the mouth of the urn is a fig-wasp (*Blastophaga grossorum*), which has escaped from one of the galls. (11) Urn-shaped inflorescence of *Ficus Carica* filled with female flowers, and divided longitudinally; at the mouth of the urn are two fig-wasps, one of which has already crept into the interior, while the other is in the act of doing so. (12) Male flower. (13) Long-styled female flower of *Ficus Carica*. (14) Gall produced by a short-styled gall-flower. (15) *Blastophaga grossorum* escaping from a gall. (16) A *Blastophaga* that has escaped. (17) The same enlarged. Nos. 1, 2, 4, 6, 10, 11, 16, natural size; No. 3, $\times 2$; No. 5, $\times 20$; Nos. 7, 8, 9, 12, 13, $\times 5$; Nos. 14, 15, 17, $\times 8$. (After Kerner.)

gall-wasps. According to Kerner ('Nat. Hist. Pl.,' Eng. Ed. 1, II, pp. 159-62), there are two forms of fig-tree that is commonly planted in South Europe, i. e. that of which the urn-shaped inflorescences contain female flowers only, and that possessing urns beset at the opening with male flowers and deeper down with gall-flowers. The former is named *Ficus*, the latter *Caprificus*¹.

As the name itself indicates, the female flowers modified to form gall-flowers do not produce fruits, but galls, which are due to a small wasp belonging to the group Chalcidiidae (*Blastophaga grossorum* *Grav.* = *Cynips Psenes* *L.*). The females of this wasp creep through the mouth of the urn into the interior of the inflorescence, and each lays an egg near the nucellus of the ovule, sinking the ovipositor perpendicularly into the style-canal of a flower. From the egg a white apodal larva develops, which feeds upon the surrounding tissue, and consequently grows rapidly, soon filling the ovary, while the ovule is destroyed. The ovary therefore becomes a gall. Pupation next takes place, and finally the small perfect insect emerges by an aperture that it has bitten in the gall, which has so far served as its abode. The males escape first and fertilize the females, which are still in the galls. These subsequently escape, and after a short stay in the urn make their way to the exterior. While creeping out, they come into contact with the male flowers near the aperture, thoroughly dusting themselves with pollen. After reaching the exterior they run (flight is rare) to younger inflorescences, make their way into them, pollinate the stigmas of normal long-styled female flowers, and lay their eggs in the short-styled gall-flowers. There is therefore a division of labour between these two forms of female flower: the stigmas of both are pollinated, and in both the wasps endeavour to lay eggs. Into the short-styled gall-flowers the eggs are thrust sufficiently deep, so that galls are developed while there is no formation of fruit. In the normal female flowers the style is so long that the eggs cannot be placed in the cavity of the ovary; hence no galls are formed, but seeds capable of germination are produced.

Kerner adds that in lower Italy, and elsewhere in South Europe where the culture of figs has been practised on a large scale from very early times, *Ficus* trees, i. e. plants in which the urns only contain seed-producing flowers, are for the most part planted in gardens because they yield the best and most juicy figs. The fig-trees of which the urns only enclose gall-flowers and male flowers, i. e. the so-called *Caprificus*, are not planted, because most of their figs soon shrivel and fall off. Only individual plants of *Caprificus* are cultivated here and there for the purpose of hanging their urns on the branches of the *Ficus*. This is called *Caprification*, and it is a prevalent opinion that when the wasps escape from the urns of the *Caprificus* and wander into the urns of the *Ficus*, the figs of the latter are improved. This opinion, although widespread among gardeners and agriculturists, is incorrect. For, Kerner continues, the figs of the *Ficus* become sweet without the aid of the wasps. As a matter of fact, excellent figs are produced from *Ficus*-urns which are not visited by wasps, and in the fruits of which no seeds capable of germination have been developed, and enormous quantities of the figs of commerce are produced quite independently of caprification. It would appear, therefore, that this custom has been handed down as a tradition from very ancient times—times when gardeners were

¹ [Cf. Laubach, 'Die Herkunft, Domestication und Verbreitung des gewöhnlichen Feigenbaums, *Ficus Carica* L. Abh. Ges. Wiss., Götting., xviii, 1882.—ED.]

concerned with the production not only of good fruit but also of seeds capable of germination for the propagation of the stock. At the present time fig-trees are no longer produced from seeds, but from cuttings, so that caprification is superfluous.

As already mentioned (pp. 64, 67-8), Hermann Müller ('Alpenblumen,' pp. 479-511) arranged entomophilous flowers in nine classes, and these must here be described at some length.

1. Pollen Flowers (Po).

These are flowers which offer only pollen to their visitors, as, e.g. in species of *Anemone*, *Papaver*, *Hypericum*, *Helianthemum*, *Rosa*, *Solanum*, *Verbascum*, and *Sambucus*. They are all very simple, regular in form (radially symmetrical), and their often very abundant pollen is usually freely exposed (Fig. 18).

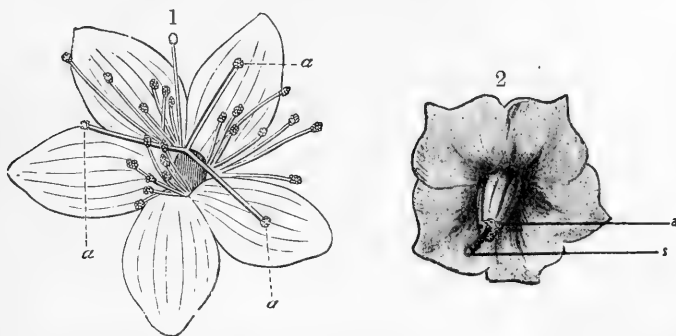


FIG. 18. *Pollen Flowers*. (1) *Hypericum*: a, stigmas. (2) *Solanum tuberosum* L.: a, anthers s, stigma.

This does not exclude the possibility of some visitors obtaining sugary juices by boring into the tissue of the base of the flower. Among pollen flowers must also be included such anemophilous plants as receive occasional visits from insects, e.g. species of *Artemisia*, *Plantago*, and *Thalictrum*, the inflorescences of which are so conspicuous that insects now and then appear as guests, and also such anemophilous flowers as possess an odour, however slight, that attracts visitors. Plants thus intermediate between the anemophilous and entomophilous types I have called 'wind flowers (W)' ('Die Besucher derselben Pflanzenart in verschiedenen Gegenden,' I, pp. 9 and 10). (Cf. p. 69, note.) *Anentomophilous* (Ane) may serve as the English equivalent.

On the other hand, nectarless flowers in which the pollen is only visible after special manipulation, e.g. *Sarothamnus scoparius*, *Genista tinctoria*, and others, are not to be regarded as pollen flowers, but are well-marked bee flowers (Fig. 19).

As Hermann Müller has explained ('Alpenblumen,' p. 479), the chief floral colours are represented among pollen flowers. The following examples illustrate this:—

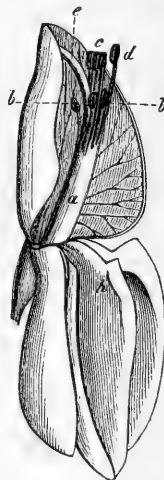


FIG. 19. *Genista tinctoria*, L. A Pollen Bee Flower (exploded). (After Hermann Müller.)

White or Yellowish-white : *Anemone nemorosa*, *sylvestris*, *narcissiflora* ; *Spiraea Ulmaria*, *Aruncus Filipendula* ; *Sambucus nigra*, *racemosa* ; *Cistus salvifolius*, and others.

Yellow : *Anemone ranunculoides* and *alpina* ; *Chelidonium majus*, *Hypericum perforatum*, *Papaver alpinum*, *Helianthemum vulgare*, *Lysimachia vulgaris*, *Verbascum Thapsus*, *Narthecium ossifragum*, and others.

Red : *Papaver Rhoeas*, *Rosa*, and others.

Lilac or Violet : *Thalictrum aquilegifolium*, *Solanum Dulcamara*.

Blue : *Hepatica triloba*.

As I have demonstrated (op. cit., p. 11), the visitors of white, yellow, and also red pollen flowers are chiefly bees and hover-flies with a short proboscis. The bodily structure and the habits of these insects sufficiently explain this fact; concealed honey is not accessible to bees with a short proboscis, and therefore they not only eagerly visit flowers with exposed or partly concealed nectar, but also pollen flowers yielding a rich booty of pollen. This substance forms a very important article of food for them, and they often carry it away from pollen flowers in great balls on their collecting-apparatus. The same holds true for hover-flies, which, as regards length of proboscis, and fitness for pollinating flowers, present the same stage of adaptation as short-tongued bees. They too are excluded from the enjoyment of nectar that is completely hidden, and pollen, which they find most abundantly in pollen flowers, is a kind of food they doubtless covet as much as nectar. It is not surprising to find honey-bees, the most energetic and industrious and perhaps the commonest of all floral visitors, upon many pollen flowers. Some humble-bees also, and various other long-tongued bees, settle upon pollen flowers, especially those which are red, violet, or blue, and load their hind-legs with pollen. The parasitic humble-bees (*Psithyrus*), which are devoid of a basket, and consequently incapable of collecting pollen, are not met with upon pollen flowers. In the Alps, where lepidoptera are numerous, they also occur as floral guests, always seeking in vain for nectar, and usually flying away after a short visit, now and then, perhaps, boring into the tissue of the base of the flower, and thus getting at some sap. Muscidae also are among the visitors, likewise seeking nectar in vain, but owing to their small perceptive powers, always coming back again. Lastly, beetles may at times appear as common floral guests, which regard the abundant pollen as welcome booty. Visitors belonging to other groups of insects do not fall to be considered in this general account.

In some pollen flowers the filaments are closely beset with hairs (*Verbascum*, *Anagallis*, *Narthecium*, *Tradescantia*), which often display conspicuous colours, and serve not only as pollen-guides to insects, but also as supports and footholds during their labour. Flowers of this kind are preferred by pollen-collecting bees.

Bee flowers too are those pollen flowers in which the anthers are united into a yellow cone closely surrounding the style and presenting a marked contrast of colour with the violet petals, e.g. *Solanum Dulcamara* and species of *Cyclamen*. The bee clambering over this anther-cone opens it, and is dusted with the dry powdery pollen that falls out. These flowers (along with nectarless lepidopterid flowers) represent the highest stage of the present group.

That *Macropis labiata* visits *Lysimachia vulgaris* almost exclusively has already

been mentioned (p. 95), also Kerner's explanation of this—i.e. that the odour characteristic of this plant is perceived only by this particular bee.

Hermann Müller regards the glowing red hue of *Papaver Rhoeas* ('Alpenblumen,' p. 479, note) not only as serving to allure insects, but also as a terrifying or defensive colour, by which grazing animals are made aware of the poisonous juices of the flower, so that they avoid it. As evidence of this assumption Müller notes that on the 'Kampen' (i.e. the enclosed meadows near Lippstadt, on which the cows pass the whole summer) the flowers of the corn-poppy remain untouched, while almost all others are grazed down. (What is true for *Papaver Rhoeas* also holds for *Ranunculus acris*.)

Certain pollen flowers are particularly noteworthy in that they exhibit a division of labour among their stamens, which enables them to make sure of crossing with fewer stamens. According to Ludwig ('Biologie der Pflanzen,' pp. 481–3) we are here principally concerned with pollen flowers possessing *two kinds of stamens with different form, but similarly-coloured anthers and pollen*—i.e. with shorter alluring stamens with *nutritive anthers* and longer alluring stamens with *reproductive anthers*. Todd, Fritz Müller, and Herm. Müller have proved for a small number of plants that this division of labour is related to *Enantiostyly*, i.e. the occurrence of *right-styled* and *left-styled* flowers (comparable to the long-styled and short-styled forms of heterostylous dimorphous flowers). *Solanum rostratum* is an example of the kind. The lowest anther in this plant is greatly elongated, and narrows into a curved point that is turned upwards at the end; the style is also upwardly curved. Both, however, are curved away from the direction of the floral axis in opposite directions. In the same raceme right-styled and left-styled flowers alternate regularly, and flowers on the same branch which *open simultaneously* are either all right-styled or all left-styled.

The humble-bees effecting cross-pollination, while stripping the nutritive anthers of the four short stamens, receive a cloud of pollen on the right side of their body in left-styled flowers, and a similar shower on their left side when in right-styled flowers. Obviously, therefore, they must always transfer this pollen on to the stigmas of flowers in which the style turns in the opposite direction. Cross-pollination therefore results in the same way as in the heterostylous flowers of *Pulmonaria*, *Primula*, and others. In *Cassia* (Caesalpiniaceae) the following relations occur:—

1. *Enantiostyly* (dextro and sinistroyly) without division of labour among the anthers—in *Cassia Chamaecrista* (according to Todd).
2. *Enantiostyly* with division of labour among the anthers, but without preferential crossing of opposite floral forms—in *Cassia neglecta* (according to Fritz Müller).
3. *Enantiostyly* with division of labour among the anthers, and regular crossing between flowers of opposite form—in *Cassia multijuga* (according to Fritz Müller).
4. Division of labour among the anthers (reproductive and nutritive) without *enantiostyly*—in a form related to *Cassia laevigata* (according to Fritz Müller).

According to Robertson, *Cassia marylandica* has three kinds of stamens. The three uppermost are reduced to dark scaly bodies, which take the place of the nectar-guides of honey flowers, and the red markings on the upper petals of *Cassia Chamaecrista*. Four stamens afford pollen to visitors, and are stripped by humble-bees. Two long stamens, one on either side of the style, are concerned with cross-pollination.

The last species forms a transition to *pollen flowers with two kinds of stamens, possessing anthers of different form and colour*. Among these are various Melastomaceae. In *Heeria*, for example, the shorter upper 'nutritive anthers' are resplendent with a dazzling yellow colour, while the reproductive stamens and the style are red, passing into violet, like the petals, with which they consequently do not contrast. We also find that the longer lower stamens have a lever-arrangement on the connective. During a visit from one of the larger bees (*Bombus*, *Xylocopa*) this keeps the anthers away while the guest is touching the style, and it is only when the insect is leaving that the pollen-mass is pressed against its body. The colour-contrast serves not only to attract insects to the more conspicuous nutritive anthers, but also at once to direct the intelligent visitor to the right place. Among the Commelinaceae, *Tinnantia undata* shows similar differentiation of the upper and lower stamens to those seen in *Heeria*. The modification of floral parts has gone somewhat further in *Commelina coelestis*. Similar division of labour and differentiation in colour are shown by the small simple white flowers of *Heteranthera reniformis*, one of the Pontederiaceae. These possess a long stamen with pale blue anther-lobes, and two short stamens with brilliant yellow pollen. In species of *Mollia* (Tiliaceae) and *Lagerstroemia* (Lythraceae), the long stamens are green, the short ones yellow. As Ludwig remarks in this connexion, the protection of pollen by inconspicuous coloration is also common elsewhere. In the nectar flowers of *Lythrum Salicaria*, for instance, the upper anthers are greenish, as also in *Echium vulgare*, where only a few of the more intelligent insects (e.g. *Osmia*) carry off the pollen. In *Echium*, however, as in other gynodimorphous plants, the anthers of the smaller female flowers, which only produce degenerate pollen, once more assume either a yellow or some other conspicuous colour, thus serving to attract insects (op. cit., p. 483).

2. Flowers with exposed Nectar (E).

The lowest stage of nectar flowers (Ne) includes those with completely exposed nectar, which is readily visible, and accessible to all visitors. Without exception they are very simple, open, and for the most part radially symmetrical (actinomorphic) flowers, generally white, greenish-yellow, or yellow in colour. The following are examples:—

White: Most Umbelliferae, *Parnassia palustris*, *Ilex Aquifolium*, *Lloydia serotina*, species of *Saxifraga*, *Sambucus Ebulus*, species of *Galium*, and others. Spotted with yellow: *Saxifraga stellaris*, *aspera*, *bryoides*.

Greenish-Yellow: Species of *Acer*, *Petroselinum sativum*, *Rhamnus cathartica*, *Euonymus europaeus*, *Alchemilla vulgaris*, *Saxifraga muscoides*, species of *Euphorbia*, *Veratrum album*; *Bupleurum falcatum*, *stellatum*, *rotundifolium*, and others; *Foeniculum vulgare*, *Listera ovata* and *cordata*, *Pastinaca sativa*, *Anethum graveolens*.

Yellow: *Chrysosplenium alternifolium* and *oppositifolium*, species of *Euphorbia*, *Saxifraga Segueri* and *stenopetala*, *Gentiana lutea*, and others. Spotted with orange-yellow: *Saxifraga aizoides*.

Pink: *Meum Mutellina*, *Pimpinella rubra*, *Gaya simplex*. Somewhat brighter red: *Azalea procumbens*.

In accordance with the position of the nectar, flowers of this class are chiefly visited by insects with a short proboscis: short-tongued wasps and flies predominate, but to these must be added beetles with equally short proboscis, and flies (Syrphidae) with proboscis of medium length, and more rarely bees with proboscis of medium length. All other insects are relatively unimportant. Even the honey-bee, so active everywhere else, is seen here comparatively seldom: apparently the small quantity of pollen and nectar offers it too little attraction, and even less to its allies with still longer proboscis. Lepidoptera, in which the long proboscis is ill-adapted for sucking up the flat layer of nectar, are extremely rare guests, even in the Alps, where such insects abound. (Cf. Knuth, 'Die Besucher derselben Pflanzenart in verschiedenen Gegenden,' I, p. 13.)

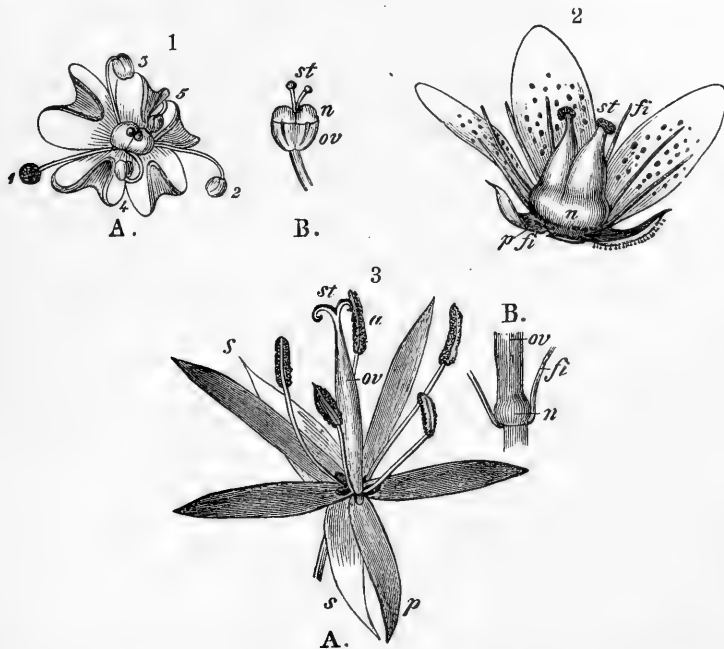


FIG. 20. *Flowers with exposed nectar.* (1) *Pimpinella rubra* Hoppe. (2) *Saxifraga aspera* L. (3) *Gentiana lutea* L. n. Nectary.

Hermann Müller ('Alpenblumen,' pp. 481-4) arrives at similar conclusions with regard to alpine flowers with exposed nectar: those which are pure yellow, yellow with orange spots, greenish-yellow, or white, are principally visited by short-tongued insects (85 % of the visitors), in particular by Muscidae, while bees and Lepidoptera are relatively very infrequent (only 15 %). The same also holds for the reddish Umbelliferae (*Meum Mutellina*, *Pimpinella rubra*), while the more intensely red *Azalea procumbens*, which secretes nectar abundantly, is mainly visited by floral guests with a more specialized sense of colour, i.e. Lepidoptera, bees and hover-flies (80 % of the visitors), while Muscidae are less numerous (20 %). In many species of *Saxifraga*, in *Veratrum*, and in *Lloydia*, the insect guests are so predominantly Diptera, that Hermann Müller (op. cit., p. 483) united them into a special group distinguished by the symbol A D (Fly flowers with fully exposed

nectar). Müller, however, expressly remarks, that a sharp limit cannot be drawn between AD and A, and that, e.g. *Rhamnus*, *Sibbaldia* and *Alchemilla* might perhaps be indicated by AD as correctly as by A. [Employing the symbols adopted in this translation— $E=A$, $F=D$, and $AD=EF$.—Tr.]

Dull yellow flowers with exposed nectar, e.g. *Anethum graveolens*, *Bupleurum falcatum*, *Pastinaca sativa*, were never seen (in Westphalia) by Hermann Müller ('Fertilisation,' p. 287) to be visited by beetles, but only by flies and bees, though Loew ('Beiträge') observed (in Silesia) six beetles among forty-six visitors of *Anethum graveolens* (13 %).

Listera ovata is chiefly visited and pollinated by ichneumons, and also by a beetle (*Grammoptera laevis*) (see 'Immenblumen,' p. 146).

Parnassia palustris is a deceptive or pseudo-entomophilous flower (see Class Fd, pp. 67-8).

3. Flowers with partly concealed Nectar (EC.)

This group is connected with the previous one by many transitional forms. The nectar is directly visible only under favourable circumstances (in bright sunshine), otherwise it is more or less hidden in the recesses of the flower. The members of this group are mostly actinomorphic, and not always fully expanded. They are completely open only in bright sunshine, while at other times they close up into hemispherical cups. They include almost all the Cruciferae and Alsineae, the species of *Ranunculus* and *Batrachium*, *Caltha*, *Crataegus*, *Berberis*, *Fragaria*, *Potentilla*, *Comarum*, *Sanguisorba*, and so forth.

In this class of flowers, white and yellow also predominate, but these colours are more intense than in the last class. White with red spots is rare (*Saxifraga rotundifolia*), so are red (*Ranunculus glacialis*) and dark purple (*Sanguisorba officinalis*, *Comarum palustre*, *Potentilla atrosanguinea*). The visitors belong to quite different groups of insects from those of flowers included in Class E. It is true that short-tongued flies and wasps, and also beetles, still constitute a considerable proportion of the floral guests, but these insects find it rather difficult to get at the partly concealed nectar, so that they prefer to visit flowers with exposed nectar. On the other hand, insects with a proboscis of medium length are extremely common pollinating-agents in flowers of this class. The simple flowers, rich in pollen, and open in the sunshine, constitute an extremely suitable field of activity for small short-tongued bees possessing collecting-bristles, as well as for hover-flies, which readily eat pollen as well as honey. These are accordingly the insects that above all others frequent flowers with partly concealed nectar, and it is interesting to see how flowers of this kind which have migrated from Europe into North America receive there a circle of guests completely comparable to the European one. According to the observations of Charles Robertson, *Stellaria media*, for example, is specially visited in Illinois by short-tongued bees and hover-flies, exactly as in central Germany.

As in the previous class, the circle of visitors of flowers with partly concealed nectar depends upon the character of the insect fauna for the particular region under observation. In districts where short-tongued bees are scarce, e.g. on the North Frisian Islands, these insects are less conspicuous than the Syrphidae: in the Alps,

where Lepidoptera abound, these are more frequent visitors than elsewhere, although the flowers of this group everywhere receive a relatively greater number of lepidopterous guests than do those of the previous group, for the nectar is here no longer so very inconveniently situated with reference to the long proboscis of such insects.

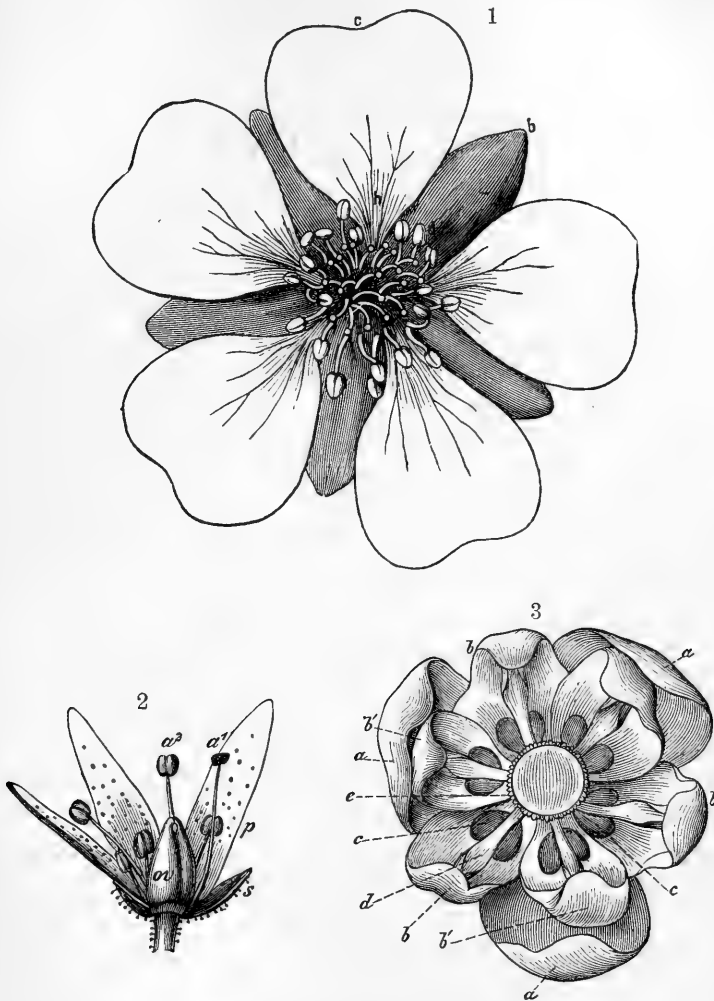


FIG. 21. *Flowers with partly concealed nectar.* (1) *Potentilla minima* Haller. (2) *Saxifraga rotundifolia* L. (3) *Berberis vulgaris* L.

The honey-bee is here met with as a much more eager visitor, and greater numbers of other long-tongued bees seek out the nectar, which is more conveniently situated for them, or collect the pollen that is usually present in abundance.

It follows that the flowers of this group, as well as their insect visitors, are in a distinctly higher stage of development than the flowers and insects of the previous class. The degree of specialization of the insects corresponds to that of the flowers

they visit (Knuth, 'Blütenbesucher derselben Pflanzenart in verschiedenen Gegenden,' I, pp. 14 and 15).

Hermann Müller arrived at conclusions similar to mine by collating his observations on the visitors of alpine flowers with partly concealed nectar. In the Alps ('Alpenblumen,' p. 487), white flowers are chiefly influenced by Diptera, while yellow ones are equally visited by Diptera and short-tongued bees.

According to Hermann Müller ('Fertilisation,' pp. 74-9 and 231-4; 'Weit. Beob.,' I, pp. 320, 321; II, pp. 241, 242), the yellow flower of *Ranunculus* and *Potentilla* are chiefly visited in central Germany by small bees belonging to the genera *Andrena* and *Halictus*—'These cross-pollinating agents correspond as completely, in size and degree of adaptation, to the dimensions and adaptational stage of these flowers as if each were made for the other' ('Alpenblumen,' p. 488).

The blackish-purple flowers of this class are almost exclusively visited by flies, and in the Alps by *Lepidoptera* as well. The way in which they resemble decaying flesh in colour is, perhaps, what specially induces flies that are fond of decomposing substances to visit them.

4. Flowers with concealed Nectar (C).

This class, again, is connected with the previous one by numerous transitional forms. The nectar is always quite out of sight of visitors, being concealed in pouches, or by hairs or projecting floral parts, so that it remains invisible even



FIG. 22. *Flowers with concealed nectar.* (1) *Trollius europaeus* L. (2) *Lycopus europaeus* L. (in outline). n. Nectary.

when the petals are fully expanded in the sunshine. Although actinomorphic forms still predominate (e.g. species of *Pulsatilla*, *Trollius*, species of *Geranium*, *Erodium*, *Cardamine pratensis*, *Cakile maritima*, *Malva*, *Rubus*, *Oxalis*, *Epilobium*, *Ribes*, *Lythrum*, *Sempervivum*, *Polemonium*, *Myosotis*, *Vaccinium*, *Calluna*, *Pyrola*, *Symphoricarpos*, *Allium*, and others), this class of flowers also includes many species exhibiting more or less well-marked zygomorphism, this indicating a higher degree of floral specialization (e.g. *Veronica*, *Euphrasia*, *Scrophularia*, *Lycopus*, *Orchis*, *Thymus*, *Mentha*, *Origanum*, and others).

White and yellow, colours which predominated in the two first classes of nectar flowers, scarcely appear at all in flowers with completely concealed nectar, but give place to reds, blues, and violets.

As I have pointed out ('Blütenbesucher,' I, pp. 16-17), not only do the flowers of this class present a considerable advance on those of the previous group, but their visitors also attain a distinctly higher level of specialization with regard to pollination than do the visitors of flowers with partly concealed nectar. The less intelligent short-tongued insects, finding it more difficult to get at nectar which is completely concealed than that which is more or less exposed, are much less important here than in the two preceding classes. Long-tongued insects, on the other hand, visit these flowers far more.

The honey-bee may almost everywhere be observed sucking the flowers belonging to this class: its proboscis (6 mm. long) conveniently reaches the nectar concealed in the base of the flower, the position of which it quickly discovers. Its nearest relatives, the humble-bees, also appear in swarms as visitors, and parasitic humble-bees eagerly seek out the abundant though hidden nectar, which they can reach without trouble, with the help of their long proboscis. The other long-tongued bees join them in this quest.

Since the nectar is usually concealed at a depth of only a few mm., it is easily reached by short-tongued bees and long-tongued wasps, as well as by the Bombyliidae and Syrphidae among the Diptera. The nectar, owing to its deeper position, can also be more conveniently sucked up by Lepidoptera than that of flowers belonging to the preceding classes.

This is more difficult for short-tongued flies (Muscidae and others) and wasps. For the same reason beetles are even more infrequent visitors: those that do occur are usually small forms, with slender bodies, enabling them to creep right into the flower, where they get at the nectar, without conferring any benefit. The coleopterous visitors are sometimes pollen-eating beetles, which only occasionally effect pollination.

Some flowers of this class are specially interesting, as being visited by definite species or groups of insects.

Wherever *Lythrum Salicaria* grows, for example (see p. 95), the bee *Cilissa melanura* Nyf. is found upon it as a guest, and indeed scarcely visits any other plant.

Symphoricarpos racemosus is in some districts almost exclusively visited by wasps, while *Scrophularia nodosa* is everywhere a well-marked wasp flower, as are *Cotoneaster vulgaris* and *Lonicera alpigena* (according to Herm. Müller's observations in the Alps). These wasp flowers will be more fully described when *hymenopterid flowers* are dealt with (cf. pp. 119-20).

Veronica Chamaedrys and a few other species of the same genus are *hover-fly flowers*, as the delicate mechanism of pollination is here only properly brought into action by flies of the kind (see Floral Class, Fb, pp. 135-6).

Not a few flowers conceal the nectar so deeply that they form a transition between classes C and H, so that they may be designated by the symbol CH, e.g. *Rubus Idaeus* and *saxatilis*; *Euphrasia officinalis*, *salisburgensis*, and *minima*; *Goodyera repens*. The following belong to CHb: *Polygala comosa* and *alpestris*, *Polemonium caeruleum*, *Vaccinium Vitis-Idaea* and *uliginosum*, *Calluna vulgaris*. *Saxifraga oppositifolia* belongs to the transitional stage CL: Hermann Müller ('Alpenblumen,' pp. 25 and 31) includes the following in CF: *Oxalis Acetosella*, *Pyrola uniflora* and *rotundifolia*.

5. Social Flowers with completely concealed Nectar (S).

Nectar is here concealed as in the preceding class, but the flowers are united into heads, so that they are not only rendered strikingly conspicuous, but there is also a possibility of several flowers being simultaneously pollinated. To this

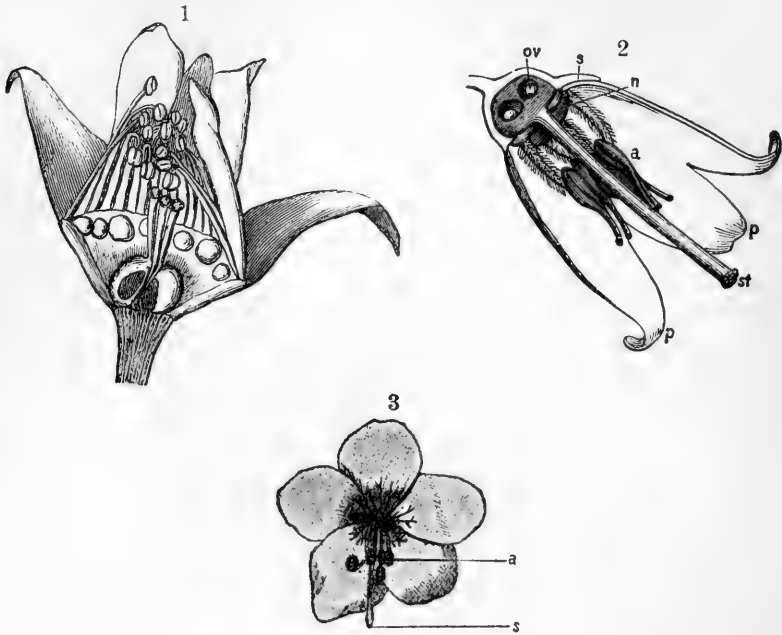


FIG. 23. *Flowers of Group CH.* (1) *Rubus saxatilis* L. (in outline). (2) *Vaccinium Vitis-Idaea* L. (in outline). (3) *Polemonium caeruleum* L.

group belong Compositae (except the anemophilous genus *Artemisia*). Here also are included species of the genera *Knautia*, *Scabiosa*, *Succisa*, and *Armeria*.

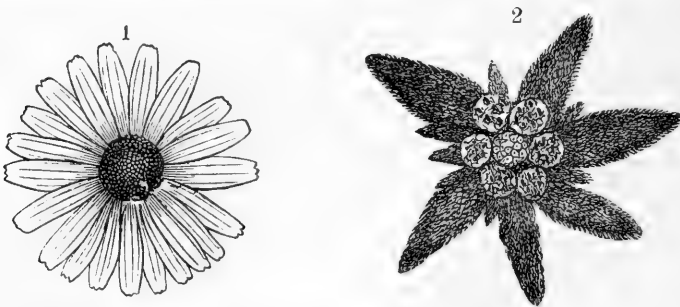


FIG. 24. *Social Flowers.* (1) *Chrysanthemum alpinum* L. (2) *Gnaphalium Leontopodium* Scop.

Social flowers fall into two sharply demarcated oecological groups: *whites* and *yellows* on the one hand, where the insect visitors are akin to those of flowers with partly concealed nectar (which are almost always of these colours), and *reds*, *blues*.

and *violets* on the other hand, where the insect visitors are practically the same as for flowers with concealed nectar, which also are almost always red, blue, or violet.

The agreement between floral colours and insect visitors in these groups can only be explained by assuming that the more highly organized insects prefer red, blue, and violet colours, from which it also follows that these colours are to be regarded as a higher stage of floral coloration.

The connection between the groups of flowers and insects above referred to, which at first appears so remarkable, thus becomes intelligible. Hermann Müller had already noticed this colour-preference on the part of insects.

In respect of frequency of insect visits, the two groups of social flowers which are made conspicuous by aggregation surpass considerably the two other floral classes that correspond to them (Knuth, 'Blütenbesucher,' II, p. 3).

As already remarked on p. 95, the little bee *Andrena Hattorfiana* F. confines its visits entirely to *Knautia*.

Transitional forms between S and L also occur. The following, for instance, belong to SL, since their visitors are almost entirely *Lepidoptera*: *Eupatorium cannabinum*; *Adenostyles alpina*, *albifrons*, and *hybrida*.



FIG. 25. *Adenostyles alpina*, Bl. et Fing., a social flower of the division SL.

6. Hymenopterid Flowers (H).

These are regularly plundered and pollinated only by Hymenoptera (membrane-winged insects). The shapes and colours of the flowers are exceedingly varied. Bilaterally symmetrical (zygomorphous) forms largely predominate, and red, blue, or violet colours. Although hymenopterid flowers are visited by insects belonging to very different groups, it is only the less specialized members of the class that can be pollinated by insects other than Hymenoptera. In the most highly specialized types

of such flowers, it may happen that pollination can only be regularly effected by a few species of bee. To this class of flowers belong the Papilionaceae, most of the Violaceae, many Labiatae, Scrophulariaceae, the species of *Aconitum* and *Delphinium*, and *Corydalis solida*, *cava*, *fabacea*, and others; also *Scrophularia nodosa*, *Lonicera alpigena*, *Listera ovata*.

They fall into five groups:—

- (a) BEE FLOWERS PROPER (*Hb*). For rifling the nectar of these a proboscis of at most 7 mm. in length is necessary (e.g. *Trifolium repens*, *Lotus*).
- (b) HUMBLE-BEE FLOWERS (*Hh*). For these a longer proboscis is required (e.g. *Trifolium pratense*, *Aconitum*).
- (c) BEE-HUMBLE-BEE FLOWERS (*Hbh*). *Calamintha alpina*.
- (d) WASP FLOWERS (*Hw*). *Scrophularia nodosa*.
- (e) ICHNEUMON FLOWERS (*Hi*). *Listera ovata*.

Owing to the great abundance of remarkable floral arrangements in BEE FLOWERS and HUMBLE-BEE FLOWERS—such as the explosive mechanism in *Sarothamnus*, *Genista*, and *Ulex*, the lever mechanism of *Salvia*, the spring mechanism of *Medicago*, and so on, only a few can be indicated here by means of figures. For a detailed account of such floral arrangements reference must be made to the second volume of this work.

The visitors of BEE FLOWERS PROPER (*Hb*) (in which a proboscis of at most 7 mm. in length is necessary to secure the nectar) include, beside honey-bees and long-tongued bees (with some of the parasitic humble-bees), a few short-tongued bees, for the slight depth at which the nectar is concealed allows them to reach it in the regular way, and so to liberate the mechanism for pollination. The same holds true for some Syrphidae, and, in the case of *Euphrasia officinalis* L., even for certain Muscidae. This last example may therefore be described as transitional between Flowers with concealed nectar and Bee Flowers. The Lepidoptera, on the other hand, are probably never able to effect pollination: their long proboscis permits them indeed to suck honey even from bee flowers, but it is far too slender to set the floral mechanism in motion. They are here, therefore, nothing but nectar-thieves. The remaining visitors are only occasional and accidental, and most of them are of no use to the flowers.



FIG. 26. *Trifolium repens*, L.
A Bee Flower.

HUMBLE-BEE FLOWERS (*Hh*) (with nectar concealed at a depth of more than 7 mm.) are almost exclusively pollinated by humble-bees and other long-tongued bees.

In certain species, e.g. *Erica Tetralix*, Lepidoptera and Hover-flies seem to be able to effect pollination when they visit the flowers. Bees with a relatively short proboscis appear only as pollen-thieves, or else steal the nectar, by biting a hole through part of the corolla, and thrusting their proboscis through it. In Germany, for instance, *Bombus terrester* L. does this to *Trifolium pratense*, *Corydalis solida* and *cava*, and *Lamium album*. Honey-bees also frequently steal nectar

through the holes bitten by this humble-bee. In the Alps, *Bombus mastrucatus* Gerst. is distinguished above all other humble-bees 'by its constant habit—destructive to the flowers—of getting nectar by forcing an entrance to deep and not easily accessible nectaries.'

Lepidoptera here again behave as in Bee Flowers proper. Other visitors are almost without exception pollen-thieves (Knuth, 'Blütenbesucher,' II, pp. 6 and 7).

Hermann Müller ('Alpenblumen,' pp. 499 et seq.) has dealt very thoroughly with the colours of Bee Flowers and Humble-bee Flowers. He calls attention to the fact that *flowers of this class which are in bloom at the same time and place*, are as a rule of *diverse colours*. Müller recalls the circumstance that several species of the same genus, with exposed or only partially concealed nectar, are often in flower beside one

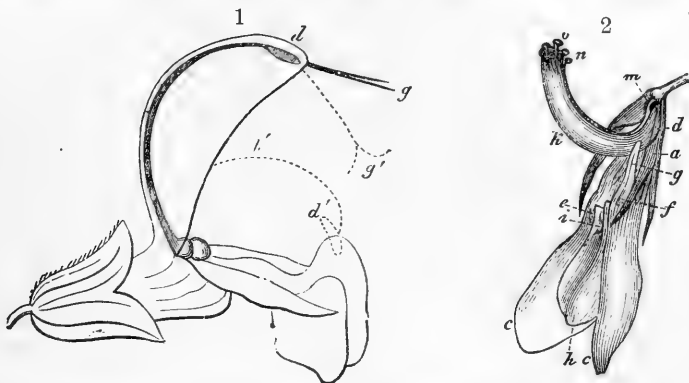


FIG. 27. *Humble-bee Flowers*. (1) *Salvia pratensis* L., a Humble-bee Flower with lever mechanism. (2) *Medicago sativa* L., a Humble-bee Flower with spring mechanism.

another at the same time, and possess the same hue, e.g. *Ranunculus acris*, *bulbosus*, and *repens*. Even, however, in the case of flowers with completely concealed nectar, accessible to short-tongued insects, similarly coloured species are in flower together, e.g. *Sempervivum*, *Mentha*, and numerous *Compositae* (especially *Cichoraceae*).

The colour relations between closely allied Bee Flowers blooming simultaneously in the same district are, on the other hand, of quite a different nature. Hermann Müller contrasts the following species with one another¹:—

Aconitum Lycoctonum—yellow; *A. Napellus*—blue;

Lamium album—white; *L. maculatum*—red; *Galeobdolon luteum*—yellow.

Salvia glutinosa—yellow; *S. pratensis*—blue.

Teucrium montanum—white; *T. Chamaedrys*—purple.

Pedicularis tuberosa—whitish-yellow; *P. verticillata*—purple.

Trifolium badium—yellow to brown; *T. montanum*—small white capitula, standing high; *T. repens*—larger white capitula, standing low; *T. pratense* var. *nivale*—still larger, dirty white capitula; *T. alpinum*—purple.

¹ Frank ('Untersuchungen über die Farben der Blüten,' p. 30, Tübingen, 1825) long ago called attention to such contrasts in colour between related species: these two contrasted colours, i.e. blue and yellow, he says, frequently appear in different species of the same genus, e.g. the genera *Linum*, *Scabiosa*, *Aconitum*, *Lupinus*, *Iris*, and others, include species with pure blue and pure yellow flowers.

Hermann Müller supposes that these different colours were evolved as a result of the possession of and necessity for discriminative powers in bees, and it does not therefore appear wonderful that not only white, yellow, red, violet, blue, brown, and even blackish (*Bartsia*) are represented in the most varied degrees among Bee Flowers, but several colours may even appear on the same flower, as in *Polygala Chamaebuxus*, *Viola tricolor*, *Cerinthe major*, *Galeopsis versicolor*, *Astragalus depressus* and *alpinus*, and so on.

A large number of yellow-flowered Papilionaceae (*Genista*, *Sarothamnus*, *Coronilla vaginalis*, *Hippocrepis comosa*) form the only exceptions. It would appear, according to Müller, that the yellow colour has here been so strongly transmitted that 'variations, which of course constitute the necessary condition for the production of different colours, may not have appeared at all.'

Various flowers of this class are visited and pollinated only by a few species of humble-bees, or even by a single species.

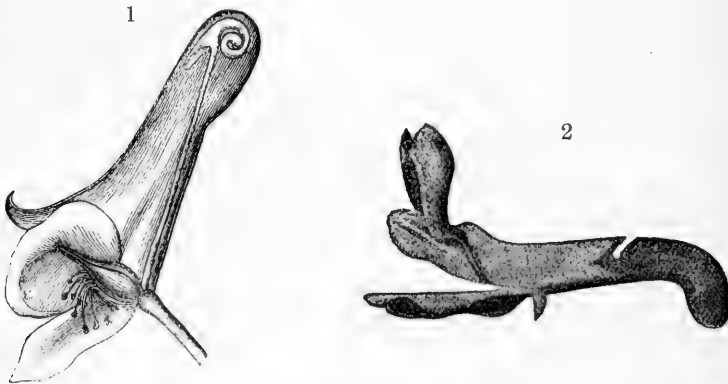


FIG. 28. *Humble-bee Flowers with Nectar concealed particularly deeply.* (1) *Aconitum Lycotomum* L. (in outline). (2) *Corydalis solida* Sm. (the corolla-tube has been bitten through by *Bombus terrester*).

Aconitum Lycotomum is of particular interest in this connection. The nectar of this flower is hidden so deeply that only insects with an exceptionally long proboscis are able to reach it.

Especially interesting is the fact that in central Germany this flower is visited exclusively by *Bombus hortorum* L., and in the Alps exclusively by *B. opulentus* Gersl. ♀. These two humble-bees possess a proboscis longer than that of any other species of the same genus living in the districts named. That of *B. hortorum* is 21 mm. long, and that of *B. opulentus* 22 mm. The latter species has hitherto been observed on no other flower. We have here, therefore, *vicarious species*.

In Jämtland (in central Sweden) C. Aurivillius (Bot. Centralbl., xxix, 1887, pp. 125 and 126) frequently observed *B. consobrinus* Dahlb. acting as a pollinator, in addition to *B. hortorum* L. Both species are 'particularly well adapted to reach the nectar.' We have here, then, a *second vicarious species*, characteristic of the 'northern alpine regions,' or perhaps it is only a vicarious variety, for Schmiedeknecht ('*Apidae Europ.*,' pp. 295, 297, 305) describes the former as a race of the latter.

Lastly, MacLeod has again met with *B. hortorum* L. as a visitor of *Aconitum*

Lycoctonum L. var. *pyrenaicum Ser.* in the Pyrenees. It may be added that this observer also saw many individuals of *Bombus Gerstaeckeri Mor.* ♀ seeking the nectar of this flower. This species (Schmiedeknecht, 'Apidae Europ.,' p. 304) is identical with *B. opulentus Gerst.* (Knuth, 'Blütenbesucher,' II, p. 7).

Another instance is afforded by *Corydalis solida* and *C. cava*. The only nectar-sucking insect effecting cross-pollination, and observed on the two species of *Corydalis* (by Herm. Müller in Lippstadt, by myself in Kiel, and by MacLeod in Ghent) was *Anthophora pilipes* ♂ and ♀, which with its long proboscis (19–21 mm.) can conveniently reach the nectar secreted and concealed in the base of the spur. 'It visits the *Corydalis* flowers in such numbers and so diligently that it suffices for the pollination of all of them.' Hermann Müller further observed two hairy hover-flies (*Bombylius major L.*, and *B. discolor Mgn.*) sucking in the normal way, though they were only nectar-thieves, and did not liberate the floral mechanism.

It is also known that *Cerinthe alpina* is pollinated exclusively by *Bombus alticola*, and *Delphinium consolida* by *B. hortorum*.

An intermediate stage between Bee Flowers and Humble-bee Flowers is constituted by Bee-Humble-bee Flowers (Hbh) which, e.g. in *Calamintha alpina*, possess two different floral forms, one of which is regularly visited by humble-bees only, while the nectar of the other is accessible even to bees with a proboscis less than 7 mm. long. In this species, according to Hermann Müller ('Alpenblumen,' pp. 319 and 320), there are large-flowered and small-flowered stocks, both of them hermaphrodite and protandrous. In the flowers of the former the corolla-tube is 10 mm. long, in those of the latter it is only 6 mm. The relations are similar in the case of *Alectorolophus major* and *minor*, which Hermann Müller regards ('Fertilisation,' pp. 454–6) as different forms of one species (*Rhinanthus Cristagalli L.*). The corolla-tube in 'major' is 9–10 mm. long, in 'minor' 7–9 mm.

WASP FLOWERS (Hw) also permit other insects to reach their nectar, and may be pollinated by them. They have, therefore, already been mentioned among flowers with concealed nectar to which they belong, so far as the shelter of nectar is concerned.

In many regions the visitors of *Symphoricarpos racemosus Michx.* are mostly True Wasps. Hermann Müller ('Fertilisation,' p. 292) observed that in Thuringia more than nine-tenths of all the visitors belonged to five species of Vespidae, while in Westphalia, where wasps are less abundant, the visits of honey-bees were more numerous. I myself noticed in Thuringia that *Vespa saxonica* was very commonly to be seen sucking nectar from snowberry flowers, while in Schleswig-Holstein (chiefly on the North Sea coast, and the Baltic coast from Rügen to Geestemünde) I observed that the visitors and pollinators of this plant¹ were almost exclusively bees and humble-bees. *Scrophularia nodosa* is a much more characteristic wasp flower. Not only in Europe, but also in North America, wasps have been noticed as the most important floral visitors of this plant. It appears, however, that this visitation is not uniform at all times of the year. In Holstein, for example, I found that this

¹ After the completion of my manuscript, I saw on July 20, 1897, at Heringsdorf, in the Island of Usedom, that *Symphoricarpos racemosus* was visited by numerous sucking species of wasps, as well as by *Apis* and *Bombus lapidarius L.* ♂.

flower was visited very eagerly by wasps at the beginning of its floral period, while later on honey-bees and humble-bees were the principal visitors. Robertson made a similar observation in Illinois, but he found that at the end of August and beginning of September, when the flowers were beginning to get scarce, wasps once more appeared as their only visitors. He concludes as follows:—‘This seems to be significant, for when any flower becomes reduced in numbers, its proper visitors are apt to be the last to leave it’ (Trans. Acad. Sci., St. Louis, Mo., v, 1891).

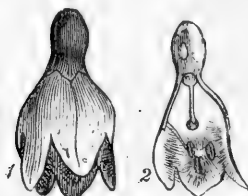


FIG. 29. *Symphoricarpos racemosus*, Michx., a Wasp Flower.

I have called attention (‘Blütenbesucher,’ I, p. 17) to the fact that the yellow anthers and brownish corolla of *Scrophularia* harmonize in a remarkable way with the colours of the insect visitors. A wasp with head inserted in the opening of the flower (which is precisely adapted to it) and projecting abdomen looks almost as if it were a part of the flower, so far as colour is concerned.

The flowers of *Lonicera alpigena* are coloured in a similar way to those of *Scrophularia nodosa* and *S. aquatica* (see Fig. 31).

According to Hermann Müller’s account (‘Alpenblumen,’ pp. 395 and 396) the flower-bud is reddish-brown. When the flower opens this colour is replaced for a short time by the dirty yellowish-white of the inner surface, while in the older flower this assumes the reddish-brown colour possessed by the outer surface. It consequently follows that the groups of flowers, taken collectively, exhibit the reddish-brown colour that is elsewhere uncommon, but resembles that which we find in *Scrophularia*. About 1 mm. above its base the corolla secretes nectar very abundantly, in a ventricose expansion, which is exactly wide enough to

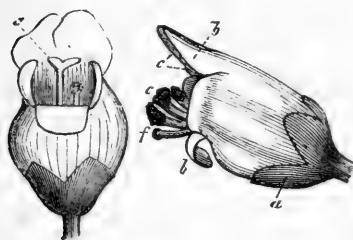


FIG. 30. *Scrophularia nodosa*, L., a Wasp Flower.

receive the head of a wasp or humble-bee. Hermann Müller observed that in the Alps two species of wasps were particularly common visitors.

The flowers of *Epipactis latifolia* also possess a similar colouring. Charles Darwin (‘Orchids’) observed that wasps (*Vespa sylvestris*) visited this species. It would appear, therefore, that the *brownish floral colour* has a very special attraction for wasps. The *ventricose nectar-pouch filled with abundant nectar* is also characteristic of wasp flowers. *Symphoricarpos racemosus*, which has already been mentioned, also possesses such a nectar-receptacle, and so does *Cotoneaster vulgaris* Lindl. (Fig. 32), which, according to Hermann Müller (‘Alpenblumen,’ pp. 214, 215), is to be regarded as a wasp flower. The small pale red flower is shaped like a hemispherical cup, of which the yellow, fleshy inner wall secretes nectar very freely, and this is sought with avidity by a wasp (*Polistes biglumis*). This insect, which cements its nest to the rocks on which the *Cotoneaster* grows, was seen by Hermann Müller to wander very frequently from flower to flower, sinking its head in the nectar-cup (that exactly corresponds in size), and thus effecting cross-pollination. Müller did not observe other visitors.

ICHNEUMON FLOWERS also appear to exist, i.e. flowers that are specially visited by Ichneumons (Ichneumonidae). These are designated by the symbol Hi. Too few of the visitors of *Listera ovata* (Fig. 33) are known to permit of a final conclusion about them. It seems probable, however, that this flower is visited almost exclusively by Ichneumons, and by a Longicorn beetle (*Grammoptera laevis*) the



FIG. 31. *Lonicera alpigena*, L., a Wasp Flower.

shape of which corresponds in a remarkable way with the form of the labellum. Sprengel ('Entd. Geh.,' p. 409) long since observed this beetle as a pollinator of *Listera ovata* in Brandenburg. Hermann Müller ('Fertilisation,' p. 530) repeated the observation 80 years later in Westphalia. Sprengel also observed numerous

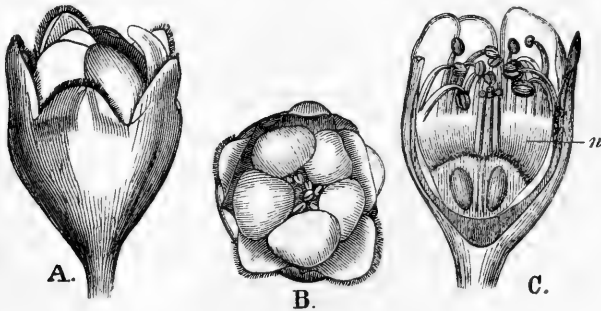


FIG. 32. *Coloneaster vulgaris*, Lindl., a Wasp Flower.

Ichneumons with adherent pollinia on the flowers in question. Darwin, Müller, and MacLeod confirmed his observation.

If, therefore, *Listera ovata* is to be regarded as an Ichneumon flower, the same may hold true for *L. cordata*, which grows in the shade of sub-alpine woods, for it

agrees with the former species in the colour, form, and arrangement of its flowers, only differing in that these are smaller. There is still, however, a necessity for direct observation to confirm this supposition, since the agents which pollinate *Listera cordata* are as yet unknown.

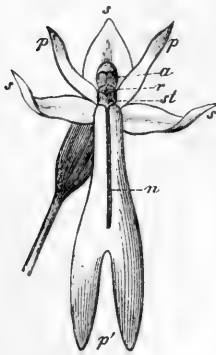


FIG. 33. *Listera ovata*, L., an Ichneumon Flower.

The two species just named belong to the class of flowers possessing exposed nectar, in connection with which they have therefore already been mentioned.

The very inconspicuous flowers of *Chamaeorchis alpina* (Fig. 34) have also an incomprehensible attraction for certain insects, for Hermann Müller ('Alpenblumen,' p. 74) found that in more than two-thirds of over fifty specimens he examined with a lens the anthers were empty and the stigmas pollinated. 'The small odourless flowers are hidden under the low grass tufts among which they grow, and which they somewhat resemble in colour, and are actually so well concealed that to avoid overlooking any of them, it is necessary to lie prone on the turf in the place where they grow, inspecting the sparsely covered surface with the greatest minuteness.'

From the flat, open position of the nectar, it follows that 'only tiny flies, beetles, or hymenoptera can be considered as agents of cross-pollination, though these have not so far been observed. Of these

the most likely visitors are certainly the Ichneumons, judging from their habits and the analogy with *Listera*, and therefore *Chamaeorchis alpina* is probably to be regarded as an Ichneumon Flower.' (Herm. Müller, Kosmos, iii, 1878, p. 480.) Müller subsequently placed this flower in a special class, that of the Small Insect Flowers (Sm) ('Alpenblumen,' p. 21).

Numerous transitional forms lead from Hymenopterid Flowers to Lepidopterid Flowers. Such intermediate types, which are crossed both by bees (or humble-bees) and Lepidoptera and which may therefore be symbolized by HbL or HhL, are very interesting because they sometimes possess

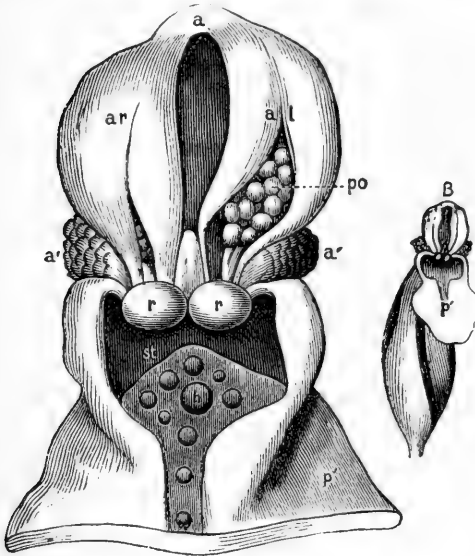


FIG. 34. *Chamaeorchis alpina*, Rich. (Ichneumon Flower?)
B. A young flower after removal of the perianth except the labellum ($\times 7$). A. Middle of the same seen from the front ($\times 35$).

two special openings, into which the proboscides of Lepidoptera and bees (or humble-bees) can respectively be inserted. *Rhinanthus Alectorolophus* (Herm. Müller, 'Alpenblumen,' p. 290; Kosmos, loc. cit., p. 419), for instance, has a wider

and longer 'humble-bee door,' and a narrower, round 'Lepidoptera door' (Fig. 35). Through the former, *Bombus alticola*, *mendax*, *mesomelas* and *pratorum* thrust their proboscis and, sucking in the normal way, effect crossing; through the latter *Colias Phocomone* and *Pieris napi* introduce their slender trunk and, also sucking in the normal way, bring about the same result.

Other Hymenopterid-Lepidopterid Flowers, usually without separate means of access for insects of the two classes, are the following:—*Gentiana obtusifolia*, *campestris*, *nana*, *involucrata*, and *tenella*; *Viola tricolor* var. *alpestris*, *Scutellaria alpina* and *galericulata*, *Oenothera biennis* and *muricata*.

7. Lepidopterid Flowers (L).

These are chiefly visited by Lepidoptera, of which the long, slender proboscis is able to reach the nectar, that is concealed in deep and narrow tubes or spurs. They fall into two groups:—

(a) BUTTERFLY FLOWERS (Lb), which are usually *red*, e. g. *Melandryum rubrum*, *Dianthus Carthusianorum*;

(b) MOTH FLOWERS (Lm), which are *white* or whitish, e. g. *Melandryum album*, *Lonicera Periclymenum*.

Lepidopterid flowers, according to my statistical summaries ('Blütenbesucher,' II, p. 8), are eagerly visited by Lepidoptera, though long-tongued bees, and even hover-flies with a proboscis long enough to reach the nectar, are also among their zealous visitors (cf. Fig. 36). The more deeply the nectar is concealed the more exclusively is it secured by Lepidoptera, among which the Hawk-moths (*Sphingidae*) are the most specialized for the purpose. It follows that 'Hawk-moth Flowers' are inaccessible to other Lepidoptera with a relatively short proboscis. In less modified flowers the visitors and pollinators are, as already stated, not so exclusively Lepidoptera, but also belong to various other insect groups, so that transitional forms can be recognized:—*Lychnis Flos-cuculi*, for example, is intermediate between Bee Flowers and Butterfly Flowers (Lb), while *Oenothera biennis* is intermediate between Bee Flowers and Moth Flowers (HLm).

Hermann Müller ('Alpenblumen,' pp. 509 and 510) came to similar conclusions. Of the thirty-three Lepidopterid flowers which he saw visited by insects in the Alps, eight were visited exclusively by Lepidoptera, i.e. *Orchis globosa*, *Lilium Martagon* and *bulbiferum*, *Gymnadenia odoratissima*; *Dianthus superbus*, *sylvestris*, *atrorubens*; *Daphne striata*. There were also eight others, apart from Lepidoptera, that were only visited by insects which did not prejudice the interests of the latter in the smallest degree, since they either made vain efforts to reach the nectar, or contented themselves with pollen. The flowers in question were:—*Gymnadenia conopsea*, *Nigritella*, *Viola calcarata*, *Lychnis Flos-Jovis* and *rubra*, *Gentiana bavarica* and *nivalis*, and *Paradisea Liliastrium*. In the other species it was mostly tiny flower-



FIG. 35. *Rhinanthus Alectorolophus*, a Humble-bee Lepidopterid Flower. *fth*, Lepidoptera door; *hth*, Humble-bee door; *st*, stigma.

beetles that penetrated into the flowers, or long-tongued flies (*Bombylius*, *Rhingia*, *Empis*) or humble-bees which managed to reach the nectar, or thievish humble-bees that broke in and carried away the spoil. It is only in a few Lepidopterid Flowers, continues Müller, that the booty is materially diminished by these intruders. This is the case, however, in *Gentiana verna*, *Silene nutans* and *inflata*, where it is due to the incursions of humble-bees, and it is particularly so in *Rhinanthus alpinus*, which is rendered useless to humble-bees by the Lepidoptera.

Hermann Müller (*Kosmos*, iii, 1878, pp. 417 and 418) called attention to a most remarkable relation between the coloration of *Butterfly Flowers* and that of

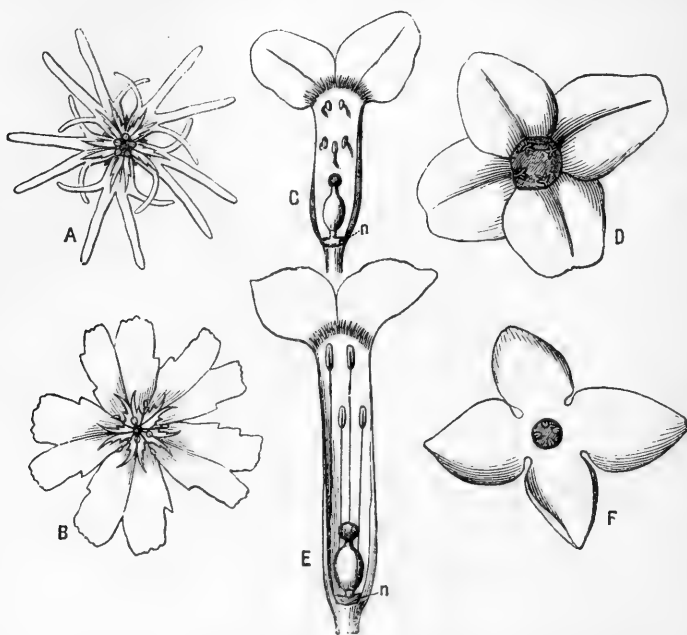


FIG. 36. A. *Lychnis Flos-cuculi*, in which the nectar is secured by long-tongued bees and hover-flies, as well as by Lepidoptera. B. *Lychnis Flos-Jovis*, in which the honey is secured only by Lepidoptera. C. D. *Daphne Mezereum*, visited by Lepidoptera, Bees, and Flies. E. F. *Daphne striata*, visited only by Lepidoptera. (After Herm. Müller.)

their lepidopterous guests. 'It is certainly not purely accidental,' says Müller, 'that most of the butterflies of the Alps, the commonest floral guests in that region, are vivid red in colour (numerous species of *Argynnis* and *Melitaea*, and several of *Polyommatus* and *Vanessa*), and that bright red flowers are visited with marked preference by such butterflies.' Müller noticed, for example, that the flowers of *Lilium bulbiferum* were exclusively visited by the fiery-red species *Argynnis Aglaja*, *Polyommatus Virgaureae*, and *P. hippothoë* var. *eurybia*, these insects being such frequent visitors that several of them often settled at once on the same flower, to which their similarity in colour at the same time afforded them the protection of invisibility. I may add, as a further example, that the Brimstone Butterfly (*Rhodocera Rhamni*), which is the commonest visitor and pollinator of *Primula acaulis*, has precisely the same colour as the flower it visits.

Many Butterfly Flowers are distinguished by an agreeable and often very powerful odour, that not infrequently resembles vanilla, and this strongly attracts the special visitors.

Moth Flowers, as Sprengel long ago stated ('Entd. Geh.,' p. 16), are white and devoid of nectar-guides (cf. p. 6). They possess, however, an odour that is frequently very powerful, and which is perceived from a great distance by the moths which visit and pollinate them. Kerner ('Nat. Hist. Pl.,' Eng. Ed. 1, pp. 208, 209), for example, narrates that during the daytime he marked a *Convolvulus Hawk-moth* (*Sphinx convolvuli*) with vermilion, and set it down at a distance of 100 metres from a honeysuckle plant (*Lonicera Caprifolium*). 'When twilight fell the hawk-moth began to wave the feelers which serve it as olfactory organs hither and thither a few times, then stretched its wings and flew like an arrow through the garden towards the honeysuckle.' When Kerner got there, he found the moth sprinkled with vermilion fluttering in front of the honeysuckle flowers and sucking nectar. It must therefore have perceived the odour of the blossoms from a distance of 100 metres.

The strong aromatic odour of the flowers belonging to this group becomes especially noticeable towards evening, while by day it may entirely or almost entirely disappear. Moth Flowers open exclusively or chiefly at dusk. The most highly specialized flowers of this group are those in which the nectar is hidden so deeply

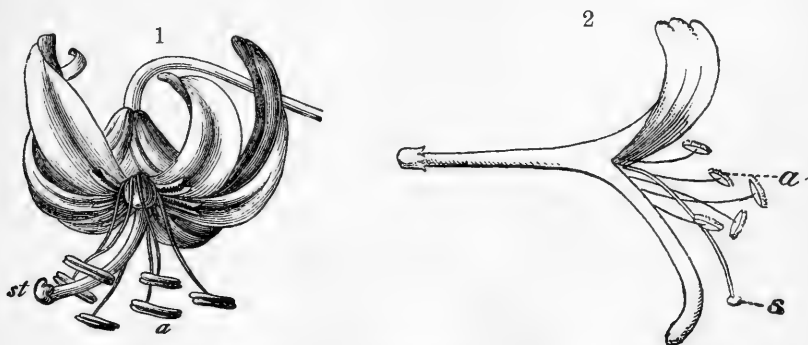


FIG. 37. *Hawk-moth Flowers*. (1) *Lilium Martagon* L. (2) *Lonicera Periclymenum* L.

that it can only be rifled by Hawk-moths (*Sphingidae*), in which the proboscis is extremely long. As these *Lepidoptera* have the habit of sucking nectar as they hover before the flower, many Hawk-moth Flowers (e. g. *Lonicera Caprifolium* and *Periclymenum*, *Lilium Martagon*) are characterized by anthers which are but loosely attached to one point of the filament, so that they readily touch the body of the moth as it hovers in front of them (see Fig. 37).

The stamens of other species of this group of flowers do not exhibit the peculiarity just described at all, or only to a slight extent, e. g. *Platanthera bifolia*, *Silene nutans* and *inflata*, and *Convolvulus sepium*.

Although the last-named species is visited during the day by insects, especially by bees, its chief pollinators are moths, of which the most important is *Sphinx convolvuli*. According to F. Buchanan White (*J. Bot.*, ii, 1873), *Convolvulus sepium* seldom fruits in England, where the *Convolvulus Hawk-moth* is uncommon, and in Scotland, where this insect does not appear to occur, the plant is very rare.

But in North Ireland, where *Sphinx convolvuli* is relatively abundant, *Convolvulus sepium* (according to T. H. Corry) is even commoner than *C. arvensis*.

There are transitional forms connecting the two groups of Lepidopterid Flowers. Hermann Müller (Kosmos, iii, 1878, pp. 420-4) regards the following as such:—*Daphne striata*, *Anacamptis pyramidalis*, *Gymnadenia conopsea* and *odoratissima*, *Crocus vernus*, and *Lilium Martagon*. The two first-named species represent all stages between Butterfly Flowers and Moth Flowers, for Hermann Müller often observed that in the same alpine stations all colour gradations between rose red and white grew side by side. Butterflies and moths alike were observed as visitors and pollinators of both species. *Crocus vernus* and *Gymnadenia odoratissima* do not fluctuate in this undecided way between Butterfly Flowers and Moth Flowers, but incline distinctly to the latter group, as their colour only varies from white to pale rose. The circle of guests, in conformity with this coloration, consists chiefly of moths.

While the four species just named show themselves to be transitional forms between Butterfly Flowers and Moth Flowers by displaying variable coloration, *Anacamptis pyramidalis* and *Lilium Martagon* do this in a different way. They possess vivid colours and thus attract butterflies, but they also open in the evening and then emit a powerful and pleasing odour, by which moths (especially nocturnal Hawk-moths) are enticed.



FIG. 38. *Crocus vernus*, L., a Butterfly and Moth Flower.

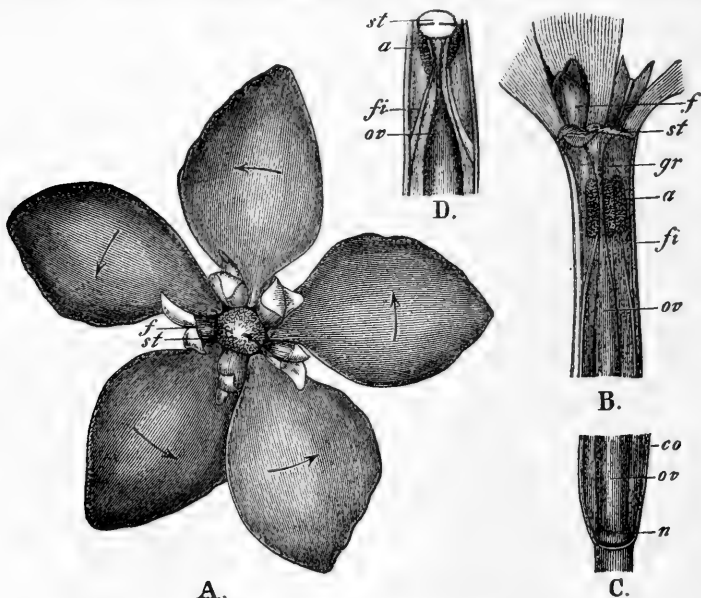


FIG. 39. *Gentiana verna*, L., a diurnal Hawk-moth Flower. (After Herm. Müller, 'Alpenblumen,' p. 340.)

Hawk-moths (*Macroglossa*) are peculiar in the fact that they visit flowers in bright sunshine. It is therefore not surprising that in the Alps, where *Lepidoptera* abound, undoubted diurnal Hawk-moth Flowers have been evolved, such as *Gentiana bavarica* and *verna* (Fig. 39).

8. Fly Flowers (F).

Fly Flowers, which are chiefly visited by flies (*Diptera*), do not constitute so clearly defined a class as those in which *Hymenopterid* and *Lepidopterid* flowers are respectively placed. They include species that are oecologically very diverse, and are in fact divided into five sub-classes: (*a*) Nauseous Flowers; (*b*) Pitfall Flowers; (*c*) Pinch-trap Flowers; (*d*) Deceptive Flowers; and (*e*) Hover-fly Flowers.

A. NAUSEOUS FLOWERS (Fn).

So far as concerns concealment of nectar, the plants here included mostly belong to the classes in which this is exposed or partly concealed. They are dull and often

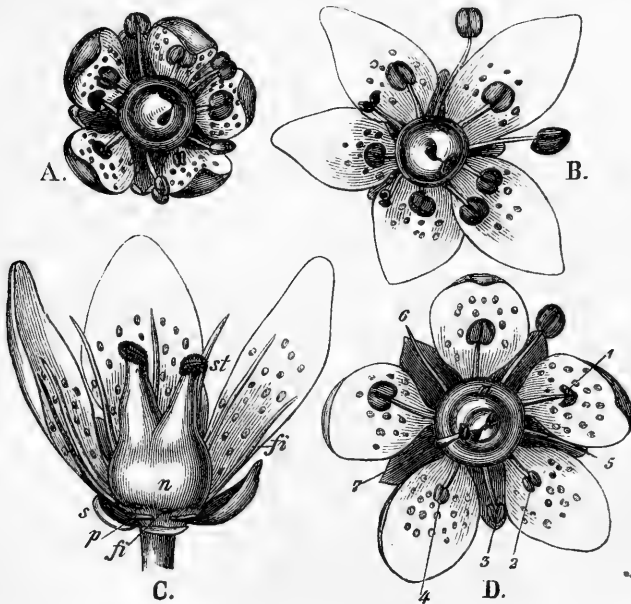


FIG. 40. *Saxifraga bryoides*, L., a flower belonging to Class EF. (After Herm. Müller, 'Alpenblumen,' p. 39.)

spotted, and yellowish or dark purple in colour. By their nauseous odour they attract many insects, especially carrion-flies and dung-flies, which are the active agents of pollination. As already mentioned (p. 109) Hermann Müller includes in this group numerous species of *Saxifraga*, in which the whitish or yellowish and often spotted flowers attract numerous flies, and he employs AD [=EF] as a group symbol for Fly Flowers with exposed nectar (Fig. 40). *Veratrum* and *Lloydia*, and perhaps also *Rhamnus*, *Alchemilla*, and others, are also to be included here.

To this group therefore belong all flowers of Classes E and EC, having 'indoloid' odours, and many that possess 'aminoid' odours (cf. pp. 91-2). Certain flowers with a 'paraffinoid' odour are also included here, e.g. *Ruta graveolens*.

B. PITFALL FLOWERS (Fpf).

A transitional stage from Nauseous Flowers, which are visited only by very small Diptera, is represented by *Asarum europaeum* (Fig. 41). The proterogynous

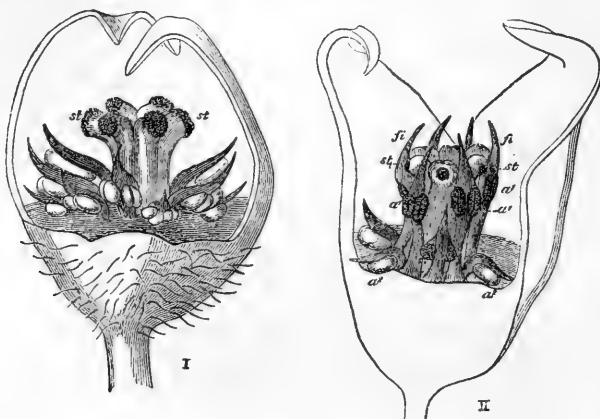


FIG. 41. *Asarum europaeum*, L. I. Young flower after removal of half the perianth. II. Older flower in outline. a^1 , Longer and, a^2 , shorter stamens; f , filaments; st , stigmas.

flowers, which are externally brownish and internally of a dirty, dark purple, smell like camphor, and entice minute flies and midges to visit them. These insects creeping about, sometimes in older flowers at other times in younger ones, effect cross-pollination. For in just-opened flowers the stigmas are already developed, standing right in the middle of the flower, so as to be touched by the Diptera that creep in. If these are already covered with pollen from a flower in the second (male) condition, pollination must result. The tips of the perianth are inwardly curved, so that the small visitors, though they can easily get into the flower, find it difficult to escape. 'It may very well happen, therefore,' says Hermann Müller (Kosmos, ii, 1877, p. 324), 'that one or other of the guests is unable to get out of the flower before the anthers have dehisced, at which time the tips of the perianth have curved more towards the exterior.' Should this occur, there is here the beginning of the development of a Pitfall Flower, and *Asarum europaeum* would thus form a transition to the remarkable pitfall arrangement of *Aristolochia Clematidis* (Fig. 42), the floral adaptation of which Sprengel ('Entd. Geh.', pp. 418-29) sketches in a masterly way, only overlooking the proterogyny and the resulting cross-fertilization. He sums up his observations in the following characteristic account:—'The flower occurs so long as it vegetates in three different conditions. After having attained its definitive size and opened, it appears to bloom, but yet actually does not do so, i.e. it is not yet ready to be fertilized, for neither are the anthers properly ripe, nor has the stigma attained to proper development. During this first condition, the

flower captures a number of flies by which it may be fertilized in its second condition. Now since, when the flower has opened, the flies do not come to it at once, as if responding to an invitation, but are led thither gradually and accidentally, it follows that this condition must naturally last for a considerable time. I have found that it continues six days. During this time chance brings to-day one fly to the flower, to-morrow two or three, and each of them, deceived by appearances, creeps in. In this way quite a considerable company of these little animals are at last gathered together, and such an unexpected meeting in so narrow a

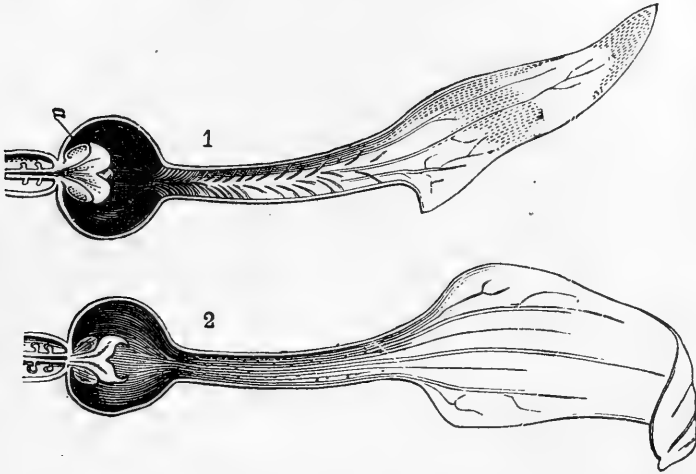


FIG. 42. *Aristolochia Clematitis*, L., a Pitfall Flower (after Sachs). (1) Flower in the first (female) condition: the perianth tube is internally beset with oblique downwardly directed hairs, the stigma is developed, the anthers (a) are closed. (2) Flower at the end of the second (male) condition: the hairs of the perianth tube are almost dried up, the margins of the shrivelled stigma are curved upwards, the anthers have dehisced.

chamber, such an undeserved incarceration in a prison so well secured, may indeed appear sufficiently strange to them. But none of them has pollen on its body, for the anthers have not yet opened. To this succeeds the second condition, in which the flower has ripe pollen, a well-developed stigma, and a sufficiency of flies to bring the former to the latter. Frequently, indeed, this may not be brought about, for here also everything is left to chance, but it must often be easily accomplished.'

'The flies, naturally enough, seeing that they have been so long walled in and have had nothing to eat, become impatient, and indignantly run about in the trap. Moreover, when they are in such a mood, conflicts cannot easily be avoided, and in these small prisons, into which the human eye cannot look, may at times go on in a tolerably warlike manner. In some such way the insects must come upon the anthers among other things, removing their pollen, carrying it about everywhere, and depositing it on the stigma, among other places. This condition cannot be of long duration. And it therefore happens that one seldom comes upon an erect flower exactly presenting it, and most of them when cut open prove to be still in the first condition. In this second condition it is often found that the flies, which are black, have something white on their backs. This is the pollen dust. As soon as Nature has attained her end, the flower passes into the third condition. It reverses its position,

and the small trap withers and disappears, so that at length the poor flies escape from their imprisonment and once more regain their liberty.'

Hermann Müller (Kosmos, iii, 1878, pp. 325-6) also considers that *Calla palustris* (Fig. 43) represents a stage leading up to Pitfall Flowers, especially to those of *Arum maculatum* (Fig. 44). Although it presents hardly any indication of transition

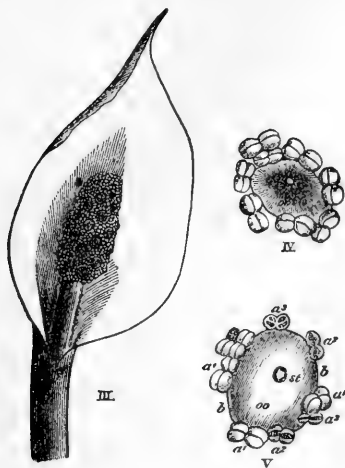


FIG. 43. *Calla palustris*, L. III. Inflorescence, somewhat reduced. IV. Single flower in the first (♀) condition. V. The same in the second (♂) condition. a^1 , closed anthers; a^2 , dehiscing anthers; a^3 , emptied anthers; st , stigma.

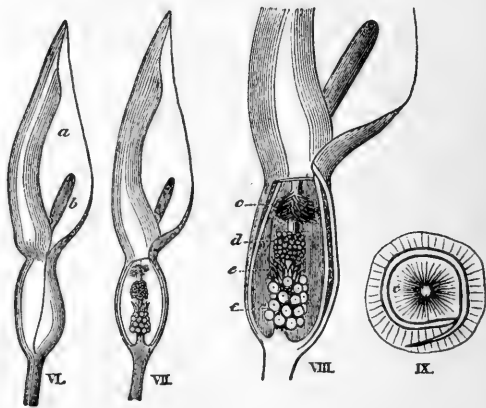


FIG. 44. *Arum maculatum*, L., a Pitfall Flower. VI. An inflorescence seen from the outside. VII. The same with flower-trap cut open. VIII. The same on larger scale. IX. Cross-section immediately above the entrance-groove: a , spathe; b , spadix; c , entrance-groove; d , stamens; e , vestigial ovaries; f , female flowers.

so far as the fly-trap is concerned, it is nevertheless one of those Nauseous Flowers—imperfectly developed, it is true—to which the disagreeable odour entices Diptera that are fond of decaying matter. Its broad, erect spathe, which is white internally, and projects far beyond the inflorescence, acts not merely by way of attraction, but also affords shelter against wind and weather to the little guests that are allured, especially when it is still half rolled up. *Arum maculatum* offers such shelter in a much safer and more comfortable way. For the spathe only opens above, so as to permit the protrusion of the dark-purple end of the spadix, which serves both as allurement and guiding-rod, while below it is closed, thus forming a pit that affords a warm resting-place to visitors. The more exact description of the entire floral adaptation is given in the second volume of this work.

C. PINCH-TRAP FLOWERS (Fpt).

The family of the Asclepiadaceae is distinguished by the occurrence of peculiar 'clips' in their flowers, which consist of small, thin, hard plates of horn-like texture, with an upwardly narrowing slit in the middle of their lower margin, and which bend towards one another along their entire length in such a way that their edges lie close together. To each such clip two pollinia belonging to two neighbouring anthers are fastened right and left by means of two cords lying in the anthers. The clips grasp the proboscides, claws, or bristles of insect visitors, and are forcibly torn away by

the insects when they feel themselves held fast. The result is that the pollinia fastened to the clips become attached to the visitors, and are thrust into a stigmatic cavity by the latter, of course unknowingly and unintentionally. The pollinia stick fast to the stigma and remain upon it to effect fertilization after the insect has released itself (see Fig. 45).

Pinch-trap Flowers are not exclusively Fly Flowers, though in species of *Vincetoxicum*, flies of moderate size, to the proboscis of which the clips attach themselves, are the agents of pollination. In species of *Stapelia* also, the clips hold on to the proboscis-bristles of large carrion-flies, which are attracted by the colour of the flowers, and by the well-marked smell of decaying flesh. Similarly, in species of *Ceropeja* the pollen is transported by small flies, and here too there are little pitfalls in the flower, as in *Aristolochia*, where visitors are retained as prisoners for a time, so that these plants form a transition stage between Pitfall Flowers and Pinch-trap Flowers.

In other Pinch-trap Flowers various other insects besides flies appear as cross-pollinating agents. On the flowers of species of *Asclepias*, for instance, are to be found, in addition to flies, bees, wasps, fossorial wasps, and Lepidoptera, to the claws or limb-bristles of which the clips remain hanging (see Fig. 46). In the species of *Arauja* the clips get attached to the proboscis of large bees, while in the species of *Stephanotis* they are affixed to the proboscis of hawk-moths, in which this organ is very long (cf. Delpino—'Relazione sull' apparecchio della fecondazione nelle Asclepidee,' Torino, 1865; and 'Ult. oss.,' Atti Soc. ital. sc. nat., Milano, xi, 1868, pp. 224 et seq.; H. Müller, Kosmos, ii, 1877, p. 330).

The species of *Cypripedium* (see Fig. 47) are also Pinch-trap Flowers, but here the whole insect is seized, not merely individual parts of the body (proboscis, claws, or bristles), as in the flowers already mentioned. The visi-

tors may partly be flies, partly the less specialized and less intelligent bees, but in our native species—*Cypripedium Calceolus*—they only consist of the latter. Hermann Müller (Kosmos, ii, 1877, p. 333), however, holds that the purple spots on the upper side of the third stamen, which is metamorphosed into a shade for keeping out light, are an adaptation originally evolved in relation to flies.

The labellum, which is deeply excavated like a wooden shoe, bears on its floor a coating of juicy hairs, and at the bases of these there are sometimes a few minute drops of nectar. Small bees of the genus *Andrena* try to get into this cavity of the

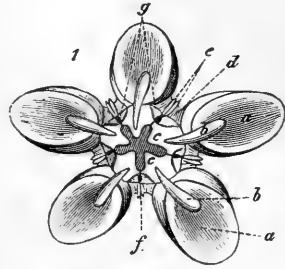


FIG. 45. *Asclepias syriaca*, L., a Pinch-trap Flower. Flower seen from above after removal of sepals and petals ($\times 3\frac{1}{2}$):—*a*, nectar reservoir; *b*, conical process of the same; *c*, upper membranous part of the stamens; *d*, outer side of the lower part of the stamens enclosing the pollinia; *e*, lateral expansion of the stamen which with the lateral expansion of the neighbouring stamen bounds the slit, *f*, in which the insect's foot and later a pollinium is caught.

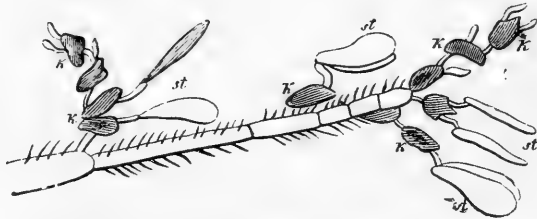


FIG. 46. Foot of a Lepidopterid with 11 clips (K) and 8 pollinia of *Asclepias curassavica*.

flower in order to feed on the sap. They use as entry the largest of the three passages leading into the cavity which lies in the middle of the gynostemium. After having fed well on the juicy hairs, they seek to pass again into the open air, but this is not possible by the opening through which they enter, because its edges are curved inwards, and are so smooth that the bees always slip down again. The two small openings at the back of the flower therefore offer the only chance of escape. To these the bee passes, pressing under the stigma and forcing itself into

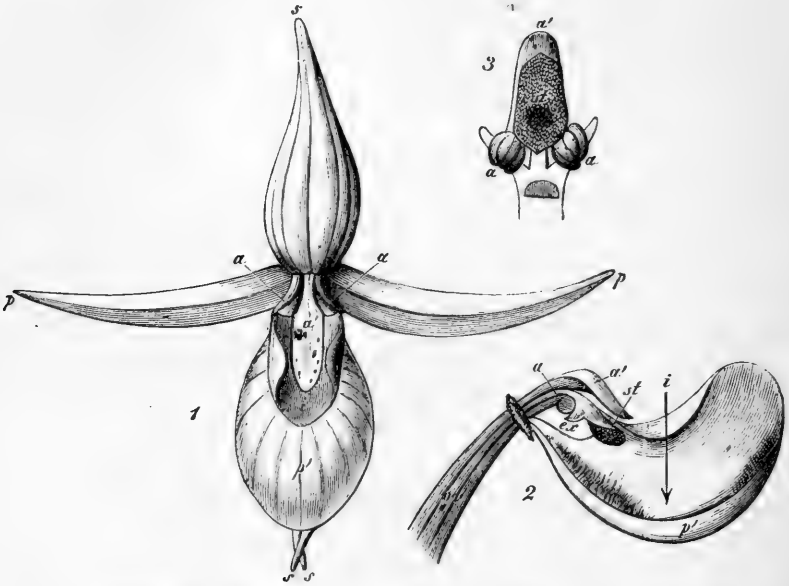


FIG. 47. *Cypripedium Calceolus*, L., a Trap-Flower. (1) Flower seen from above and in front. (2) The same in longitudinal section, after removal of the sepals and the two upper petals. (3) Anthers and stigma seen from below: *a*, anthers; *a'*, metamorphosed stamen; *s*, sepal; *p*, petal; *p'*, specialized petal (labellum); *st*, stigma; *i*, entrance; *ex*, exit.

one of the two little exits. In doing so it covers its shoulder with the sticky pollen of that anther which forms the inner margin of the exit selected. The bee carries the pollen with which it has been thus loaded to the next flower visited, applying it to the stigma in the manner described.

The four or five exotic species of *Cypripedium* investigated by Delpino ('Ult. oss., Atti Soc. ital. sc. nat., Milano, xi, 1868, pp. 175 et seq., xii, 1869, pp. 227 et seq.) are Fly-trap Flowers with the same arrangement as *Cypripedium Calceolus*. According to Delpino (op. cit.) *Selenipedium* is also a Fly-trap Flower of similar construction to *Cypripedium*, 'but with this difference, that the two upper of its three floral leaves are modified into dependent tails about half a metre long, and these, like other similar structures (e.g. in *Himantoglossum hircinum*), appear to serve as guide-ropes to the visiting Diptera.' (Kosmos, ii, 1877, p. 333.)

Pinguicula alpina (Fig. 48) possesses a Fly Pinch-trap which is quite different from the arrangements of *Asclepiads* and *Cypripedium*, and which Hermann Müller describes at length in his 'Alpenblumen' (pp. 352-4):—

The white flowers, ornamented at their entrance with two yellow sacs (*a*) covered with yellow hairs, chiefly attract medium-sized flies, which creep in bodily till their heads project into the hollow spur (*c*). This is devoid of nectar, but on the inner surface of its lower side there are small unicellular capitate hairs, and the contents of the juicy heads of these appear to serve as food for the dipterous visitors. The stiff hairs directed obliquely backwards, that occur at the entrance to the spur (at *b*), permit the flies to thrust in their heads with ease, and further serve them as a convenient resting-place, but also prevent the head from being rapidly withdrawn. This can only be gradually effected by the fly pressing its body upwards as far as possible from among the blockading hairs that grasp it. In doing this it touches the anthers with its back, folding forwards and upwards the stigmatic lobe that covers them. The flowers being protogynous, the fly regularly effects cross-pollination,

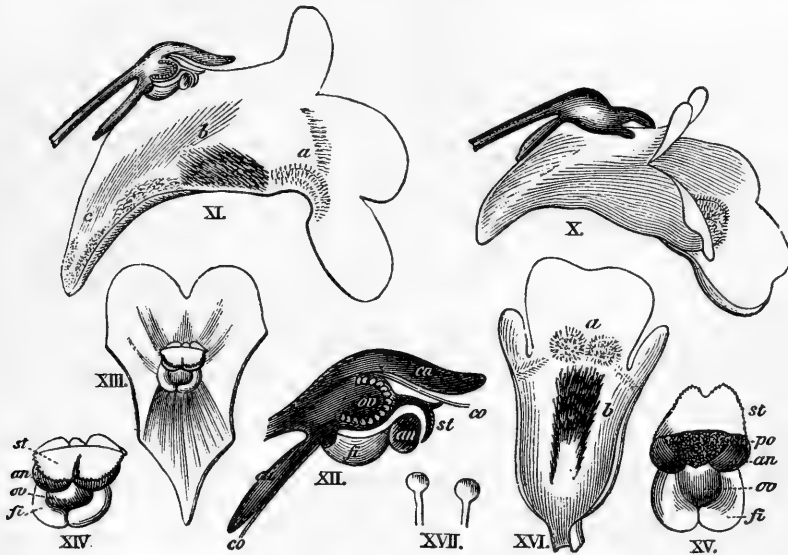


FIG. 48. *Pinguicula alpina*, L., a Fly Pinch-trap Flower (after Herm. Müller). X. Flower seen from the side. XI. The same in longitudinal section ($\times 3\frac{1}{2}$). XII. Sexual parts of the same ($\times 7$). XIII. Upper half of flower with anthers still closed ($\times 3\frac{1}{2}$). XIV. Sexual parts of the same ($\times 7$). XV. Sexual parts of a flower, of which the anthers have dehiscent. The lower stigmatic lobe is folded upwards from behind, so that its under-surface is visible. XVI. Lower half of the flower. XVII. Two of the capitate hairs, with which the inner wall of the spur is clothed ($\times 80$).

applying the pollen of the older flowers to the stigmas of the younger ones. Such flies as are large enough to be gripped, but too feeble or clumsy to withdraw in the proper way, remain sticking and perish by starvation. *Pinguicula alpina* is therefore, as Hermann Müller (op. cit.) states, a plant that seizes and kills insects in two different ways. On the one hand, it grips flies with its flowers, and if these are clever enough to free themselves from the claspng bristles they serve as agents of cross-pollination, but otherwise fall sacrifices to their unskilfulness. On the other hand, the plant captures all kinds of small insects by the glandular secretion of its foliage leaves, and afterwards digests them.

D. DECEPTIVE FLOWERS (Fd).

Parnassia palustris everywhere proves itself to be a Deceptive Fly Flower¹. Sprengel ('Entd. Geh.,' p. 167) confesses that he finds the greatest difficulty in interpreting the 'five sap-producing arrangements, which in alternation with the stamens surround the pistil, and of which the structure is quite original and of its kind unique.' We are indebted for a solution of the problem to Hermann Müller, who ('Alpenblumen,' p. 112) writes somewhat as follows:—'The yellow balls at the end of the slender outgrowths from the staminodes resemble drops of fluid so completely that we are obliged to convince ourselves by a special test that they are not such, but that we have to deal with perfectly dry swellings. *Parnassia palustris* thus appears to hold up to the view of the "stupid flies" some fifty² drops of nectar visible from afar, by which they are strongly attracted. When they approach, how-

ever, the flowers offer but a very modest booty of exposed nectar, in comparison to the prospect held out. In fact the "stupid flies," i.e. the Muscidae, are everywhere the chief visitors, for astuter insects perhaps allow themselves to be deceived once, but do not so readily return.' That this interpretation is the correct one, is shown by an observation of Hermann Müller, jun., who, for a considerable time and from no great distance, watched a hover-fly (*Eristalis nemorum*), which is one of the more sagacious Diptera, while it attempted to lick these apparent drops, and it was only frightened away by the closer approach of the observer.

Ophrys muscifera also appears to be a Deceptive Fly Flower. Its purple-brown

velvety labellum, says Hermann Müller (*Kosmos*, ii, 1877, p. 335), with its pale-blue naked spot, seems exactly as if made to entice, by its colour, flies with a taste for decomposing material. Under favourable circumstances a broad median longitudinal stripe on the labellum, which includes the pale-blue spot, is covered with numerous little drops, that Hermann Müller saw a flesh-fly (*Sarcophaga*) licking. The two shining black tubercles at the base of the labellum, that look like two drops of fluid, are regarded by this investigator as pseudo-nectaries, which cannot fail to tempt a fly that has approached to try to suck them, thus bringing about the first act of cross-pollination. For as the insect stoops down to one of the two pseudo-nectaries, it can scarcely fail to touch with its head the projecting rostellum, thus causing the adhesion of a pollinium, and when a few minutes later

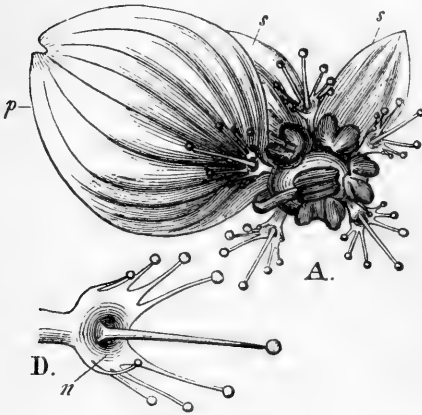


FIG. 49. *Parnassia palustris*, L., a Deceptive Fly Flower. A. Flower after removal of three sepals and four petals, seen exactly from above ($\times 5$). D. Staminode (highly magnified). n. Nectar.

¹ Cf. the note on *Parnassia* in Vol. II.

² In vigorous plants in the Meimersdorf Moss, near Kiel, I saw each of the five staminodes ornamented with about twenty-five balls, so that the flowers possessed as many as 125 apparent nectar-drops.

the insect alights upon another flower, to be once more deceived, the pollinium sticking to its head has in the meanwhile curved downwards in such a way that it will strike the stigma, and thus effect pollination.

A final example is afforded by *Paris quadrifolia*, which has been recognized as a Deceptive Fly Flower by Hermann Müller (Kosmos, ii, 1877, p. 336). The offensive odour at once suggests that flies are the visitors. In the middle of the flower, the dark purple pistil, which is crowned by four stigmas similarly coloured, shines as if it were wet with fluid and thus entices flies that like decomposing substances, e.g. *Scatophaga merdaria* *F.* To such insects the idea is suggested that here may be found the putrid matter they eagerly desire. The four greenish-yellow linear petals hang down like narrow lappets from the flower, often almost far enough to touch the four foliage leaves. They are regarded by Hermann Müller (op. cit.) as guide-ropes for small gnats, which are led by them into the middle of the flower to the deceptive ovary. The erect stamens surrounding the centre of the flower, are thought by this investigator to serve as perches up which the flies creep, and so get covered with pollen. On several occasions Hermann Müller actually observed a small gnat (*Ceratopogon*?) and a few Muscidae (among them *Scatophaga merdaria* *F.*) flying to the flowers, and busying themselves chiefly with the ovary,

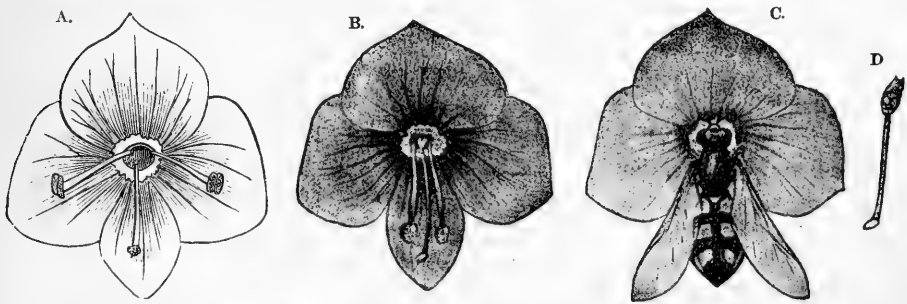


FIG. 50. *Veronica Chamaedrys*, L., a Hover-fly Flower. A. Flower seen from the front. B. The same with stamens placed together. C. The same with *Ascia podagrica* *F.*, which has drawn the stamens together under its body, in the manner indicated in B. D. Pistil with nectaries ($\times 3$).

and sometimes with the stamens. But the little insects were so shy that it was only possible to observe them from a distance, and the entire sequence of their operations in the flowers could never be seen. Hermann Müller concludes from his observations that at least the most important part of the process may be considered settled, i.e. that the pistil, although it offers no food, serves to entice certain Diptera, so that *Paris* belongs to the Deceptive Flowers. This greatly increases the probability of the interpretation given above in respect of the floral adaptations of *Ophrys muscifera* (Kosmos, ii, 1877, p. 337).

E. HOVER-FLY FLOWERS (Fh).

Hover-fly Flowers are beautifully coloured, marked by radiating streaks and possessing a decorative, sharply defined centre. Their delicate mechanism for pollination is put into action by hover-flies as elegantly coloured as themselves.

Veronica Chamaedrys will serve as a typical example. The bright blue flowers are streaked with darker lines, and ornamented in the middle with a paler nectar-guide. They are united into moderately conspicuous inflorescences, and are homogamous. The style with its terminal stigma projects obliquely downwards

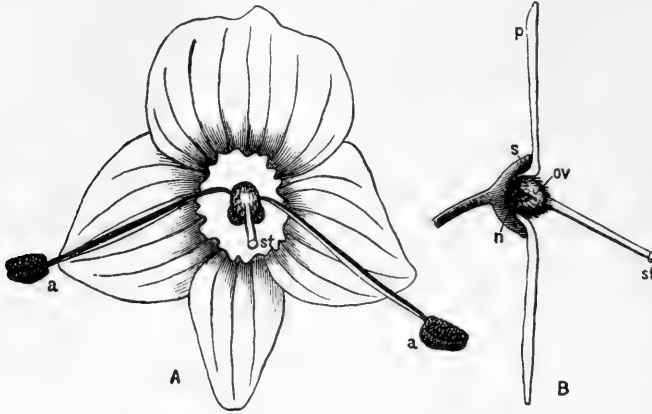


FIG. 51. *Veronica latifolia*, L., a Hover-fly Flower. A. Flower seen exactly from the front ($\times 7$), B. The same seen from the side, after half of it has been removed ($\times 7$): *s*, sepals; *p*, petals; *n*, nectary; *a*, stamens; *st*, stigma.

out of the middle of the flower where nectar is produced, while the two stamens diverge from each other to right and left. The filaments are narrowed at their bases and can therefore be easily turned inwards. Small variegated Syrphidae (*Ascia podagrica*, *Melanostoma mellina*, and others) first hover for a second in front of the flower, delighting in its beautiful colour, and then settle on its centre, thus coming into contact with the projecting stigma. In order to obtain a firm hold, they first grasp the filaments with their fore-legs, and immediately afterwards with their middle and hind-legs, and before one has time to see it they have unconsciously brought together the two stamens under the ventral side of the abdomen, and dusted that region with pollen, which is deposited on the stigma of the next flower they visit (Fig. 50).

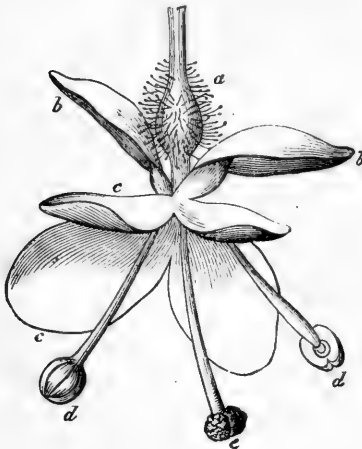


FIG. 52. *Circaea luteoliana*, L., a Hover-fly Flower. The flower is seen obliquely from above. *a*, ovary; *b*, sepals; *c*, petals; *d*, stamens; *e*, style with stigma.

This striking floral mechanism also occurs in a few other species of the genus *Veronica*, though in some of them it is not so highly perfected, e.g. *V. longifolia*, *montana*, *latifolia* (= *urticifolia*). (See Fig. 51.)

Our native species of *Circaea* present the same adaptation to hover-flies, for it is only insects of this kind that bring their floral mechanism into action in the proper way.

9. Flowers pollinated by Small Insects (Sm).

Hermann Müller ('Alpenblumen,' pp. 510, 511) places in this category flowers that are visited and cross-pollinated by *small* insects belonging to various orders. *Herminium Monorchis* may be named as a type of the group. Its minute greenish-yellow flowers, possessing, however, a powerful odour, were observed by George Darwin to be visited by equally small Hymenoptera, Diptera, and Coleoptera, while Hermann Müller adds tiny Ichneumons (Braconidae and Pteromalidae) to the list of visitors. When these little creatures, which are only 1-1½ mm. long, creep

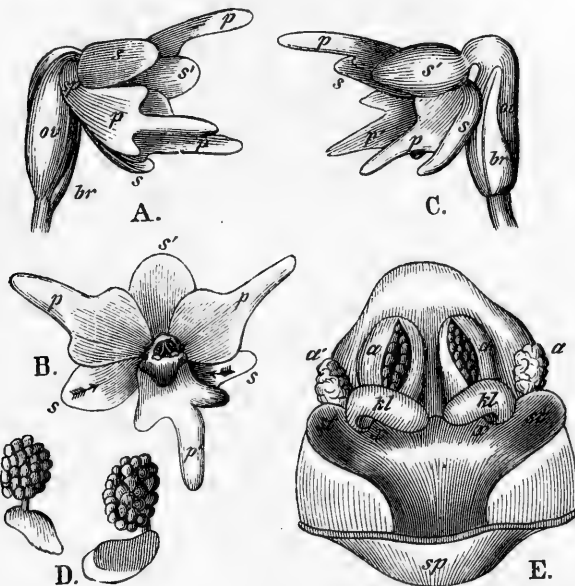


FIG. 53. *Herminium Monorchis*, R. Br., a Small-insect Flower (after Hermann Müller). A. Flower seen from the right side ($\times 7$). B. The same with floral leaves completely spread out, seen from the front. C. The same showing the natural position of the parts as seen from the left side. D. Pollinia ($\times 32$). E. Sexual organs and base of the labellum ($\times 32$). *s*, Outer perianth leaves; *p*, inner perianth leaves; *a*, anther-lobes; *a'*, vestiges of the other stamens; *st*, lobes of the stigma; *ov*, ovary; *sp*, spur; *br*, bract; *kl*, rostellum; *x*, under-side of the same.

into the flower (in the direction of the arrow in Fig. 53), and linger at the nectary, the pollinia get cemented to them, and are carried to the stigma of the next flower visited.

Perhaps *Chamaeorchis alpina*, which has already been mentioned (see p. 122) among the Ichneumon Flowers, would more properly be placed in the present group.

IX. Insects that visit Flowers.

If not only the *Colour* of flowers, but also their *Odour* serves as an allurement to insects effecting cross-pollination, these insects must possess well-developed *olfactory organs*, as well as acute organs of sight. There are, in fact, many indications that their antennae are the seat of the olfactory sense. The sensory structures here occurring are either confined to the ends of individual joints, sometimes the

terminal ones, or scattered over the whole surface of the antennae, and consist of bristle-like or conical hairs, pits, and membranous canals.

According to Kolbe ('Einführung in die Kenntnis der Insekten,' pp. 432-5) the following are the facts with regard to the development of olfactory organs in the various orders of insects.

Butterflies and Moths possess on their antennae projecting sensory hairs, simple chitinous pits with a single sensory cone, and also large pits with many

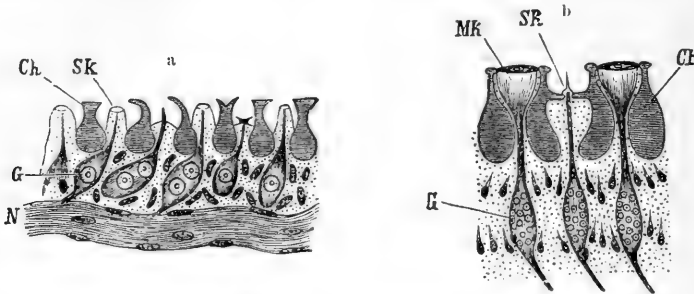


FIG. 54. *Olfactory organs of Insects.* *a*, Transverse section through the wall of the antenna of the Cockchafer. *N*, nerve; *Ch*, chitinous membrane; *G*, ganglion-cell of the sensory cone (*Sk*) sunk in a pit. *b*, Section through the antenna of *Cetonia aurata*. References as in *a*. (After O. vom Rath.)

such cones. The sensory hairs are large, pale, chitinous tubes, which are generally somewhat curved, and more or less tapering. The simple pits present a great variety in structure and are generally distributed, while the pits with many sensory cones are found only in certain genera. Hawk-moths possess the most specialized olfactory organs, and Kerner (cf. p. 125) has made observations with regard to the delicate sense of smell possessed by these insects.

Upon the antennae of **Beetles** are to be found superficial sensory cones and sensory bristles, together with membranous canals and chitinous pits (Fig. 54).

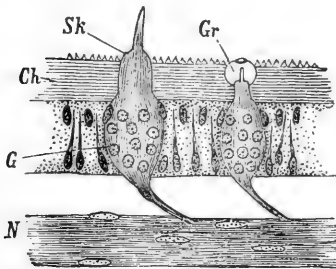


FIG. 55. *Olfactory organs of Gomphocerus rufus.* Part of a longitudinal section through the antenna. *Ch*, Chitinous membrane; *Sk*, sensory cone; *Gr*, sensory pit; *G*, ganglion; *N*, nerve. (After O. vom Rath.)

The number of these little sensory pits is particularly large in carrion-loving beetles (*Silpha*, *Necrophorus*, *Staphylinus*, &c.). In the cockchafer there are 39,000 such pits on the antennae of the male, and 35,000 on those of the female. No pits have hitherto been found in the *Carabidae*, *Cerambycidae*, *Chrysomelidae*, *Curculionidae*, and *Cantharidae*.

Hymenoptera possess membranous canals, various forms of cone, and pointed sensory hairs (Fig. 55). Besides these structures, Forel has found 'flasks' and 'champagne-cork organs' in the skin of *Ants*, *Humble-bees*, and *Bees*. These also are of sensory nature. The 'champagne-cork organs' of humble-bees and bees are confined to the terminal joint,

¹ [These structures were previously described by Hicks, 'On the Organs of the Antennae of Insects,' Trans. Linn. Soc., London, xxii, 1857.—TR.]

while the 'flasks' occur in various parts on the distal joints. Such 'flasks' are found in *Apis*, *Bombus*, *Eucera*, *Xylocopa*, and *Anthophora*. The olfactory pits and olfactory cones vary greatly in number. In honey-bees there are 14,000 to 15,000 pits, and some 200 cones on each antenna.

Among **Diptera** there are chitinous pits containing sensory cones, and of very varied forms. The pits are sometimes simple, with only one cone; sometimes compound, with a larger number (up to 100) of cones. The *Tipulidae* possess isolated cones only, while both kinds are present in *Tabanidae*, *Asilidae*, *Bombyliidae*, *Leptidae*, *Dolichopodidae*, and *Stratiomyidae*. In the other families there are only aggregated cones. In the flesh-flies and dung-flies there are 60 to 150 pits, in *Trypeta* and others only 2 to 5 on each antenna.

A few of the **Neuroptera**, **Orthoptera**, and **Hemiptera** also possess pits or sensory cones on the antenna.

The centre of the olfactory sense of insects is to be sought at the base of the antennary nerve. At its point of origin occur peculiar rounded masses, the olfactory bodies, which are so described.

As there is a well-developed sense of taste in many insects, it may be deduced that they also possess special *gustatory organs*, since in the case of odourless substances taste is only possible when these are touched by the mouth-parts of the insect, its seat must be in the region of the mouth. Sensory pits with nerve-endings are actually found (Kolbe, op. cit., pp. 442-5) both in the walls of the mouth-cavity as well as on the tongue and palps. These must at once come into contact with the food that is taken. On the proboscis of a fly, for example, organs of taste are found, together with tactile hairs. The interior of the tubular proboscis of a butterfly or moth is regularly beset with small chitinous cylinders, which project into its cavity, undertaking a quantitative and qualitative examination of the fluid nourishment taken in. At the base of the tongue in bees and similar insects there are little chitinous pits on either side, which are regarded as gustatory organs. At the tip of the ligula and on the under-side of the first maxillae of some Hymenoptera (ants, wasps, bees) sense-organs (Fig. 56) are also present. The paraglossae of the honey-bee and humble-bees also possess similar taste-organs.

It is a familiar fact that insects possess *compound* or *faceted eyes*, the peculiar structure of which is explained by their immobility and the slight power of movement possessed by the head. If insects were equipped with a single refractive apparatus like the eyes of a vertebrate, but immovable, this would need to be very strongly convex, and very prominent, to enable its owner to see at the same time objects in front and around. But such an arrangement would make distinct vision impossible on account of the well-known principle of spherical aberration. When eye and head are immovable, clear vision can only be attained by division of the eye into a number of radiating cones, capable of making isolated and independent observations, and so arranged that rays of light, from any object within the field

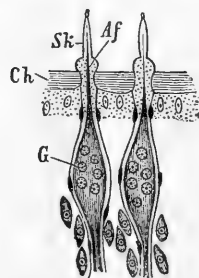


FIG. 56. *Taste-organs of Insects.* Sensory cone (*Sk*) from the tip of the ligula of *Vespa vulgaris*; *Af*, axial thread. (After O. vom Rath.)

of vision, must fall upon one or several of them in the direction of their axes. A faceted eye, the surface of which frequently occupies more than a hemisphere,

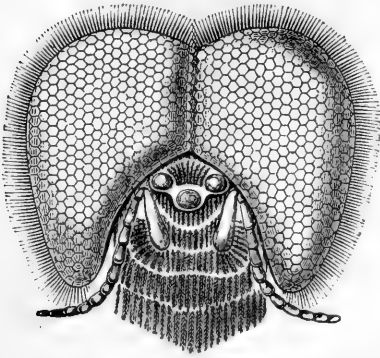


FIG. 57 a. Head of a Drone seen from the front, showing the compound eyes, the three ocelli, and the antennae. (After Swammerdam.)

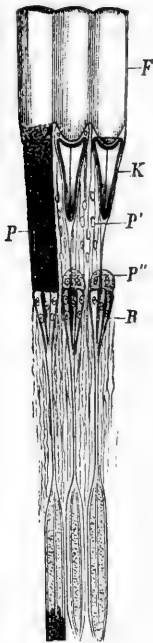


FIG. 57 b. Three facets with retinulae from the compound eye of the Cockchafer: the pigment has been removed from two of them. *F*, corneal facet; *K*, crystalline cone; *P*, pigment sheath; *P'*, pigment cells; *P''*, pigment cells of the second order; *R*, retinulae. (After Grenacher.)

consists firstly of a number of hexagonal, transparent *corneae*, or *facets*, which, while moderately flat externally, frequently present lenticular prominences internally, and are separated from one another by shallow grooves. Behind each cornea there is a transparent refractive organ—the *crystalline cone* surrounded by a dark, funnel-like, pigment sheath. Internal to these two zones is the third and last layer, that of the *visual rods*. The narrow, stalk-like, internal end of the crystalline cone is enclosed by a funnel-shaped depression at the external end of the visual rod, so that the two are directly connected. The large compound visual rods make up a hemispherical *retina* convex externally, and this extends to the bulbous expansion of the optic nerve, which receives external impressions and transmits them to a ganglion corresponding to the brain of higher animals, where they result in sensations.

Each facet, therefore, with its visual rod forms an independent eye, connected with others only by means of the common nerve-trunk. If, now, a reversed and reduced image of the surroundings is formed behind each facet (Gottsche), which is convex internally, this image is remote from the irritable part of the visual rod, and only its vertically incident axial ray (strengthened by refraction) can be perceived, as all the lateral rays are absorbed by the pigment. The impressions produced by such axial rays, the number of which corresponds to that of the individual nerve-rods, consequently form a kind of mosaic, which repeats upon the retina the arrangement of the points of the external object from which light is received. The picture thus pro-

jected, however, is deficient in brightness and detail (Claus, 'Lehrbuch der Zoologie,' 5th ed., 1891, p. 84).

This theory of *Mosaic Vision* in insects was propounded as early as 1826 by Johannes Müller, the Berlin physiologist. Its correctness was afterwards doubted, and the suggestion was made that each component of the compound eye receives a complete but reversed image of the external object, so that the insect perceives the object as many times as there are facets (Gottsche, 1852). More recent investigation (Grenacher, 1879; Exner, 1875, 1881, 1889, 1891) showed this theory of *Multiple Vision* or *Theory of Images* to be untenable, and Müller's theory of mosaic vision to be correct. The theory has undergone, however, an important modification, it now being believed that a number of crystalline cones are concerned in the perception of each point of light, so that in consequence of refraction, a dioptric but erect picture results (Claus, op. cit., p. 569).

The insect, therefore, perceives only a part of the object by means of each facet and, since each facet sees a different part, the result is a compound, mosaic, erect picture.

There is a great deal of variation as to the number and size of the facets, but the numbers appear to be tolerably constant within the various orders of insects. The house-fly, for example, possesses about 4,000 facets, the goat-moth (Cossus) 11,000, the death's-head-moth 12,000, some Neuroptera 12,000, a dragon-fly (Aeschna) 20,000, and a beetle (Mordella) 25,000. Since the recognition of an object is only possible by the summation of the separate activities of the individual facets, distinctness of vision is in proportion to the number of facets (Exner). The smaller the facets and the longer their crystalline cones, the fewer (but at the same time the more definite) are the rays of light which affect them, and the more limited are the parts of the outer world which can be perceived. The larger the facets and the shorter their crystalline cones, the more numerous (and the more intense and widely distributed) are the effective rays of light, but at the same time perception is more diffuse. Many small facets diminish the intensity of light, but increase the distinctness of vision, or power of localization. If the whole eye is strongly curved it receives light from many different directions, and the field of vision is enlarged. At the same time fewer facets are met by the rays of light from one and the same point of an object, and so the field of vision of one facet is more sharply marked off from that of others, and is consequently more distinct.

It follows from these views of Exner that insects which fly in darkness (e.g. moths) possess larger and more strongly curved facets than diurnal insects (e.g. butterflies).

It appears from the calculations of Notthafft that insects cannot recognize clearly objects which are more than 60 cm. away, so that they are extremely *short-sighted*. Beyond the limit named vision is dim, though movements, both of light or dark objects, can be distinguished at greater distances. According to Plateau the visual range of insects never greatly exceeds 2 m. On an average, Lepidoptera can see the movements of a large body at 1.5 m., flies at 0.8 m., and Hymenoptera at 0.5 m. Plateau is therefore of opinion that insects are guided to flowers exclusively by the sense of smell.

That insects are short-sighted is confirmed by the observations of Delpino ('Ult. oss., Atti Soc. ital. sc. nat., Milano, xii, 1869, p. 10). On a meadow near

Vallombrosa plants of *Bellis perennis* and *Anemone nemorosa* grew in equal numbers, and were distributed at equal distances from one another. Delpino saw a bee collecting pollen from the *Anemone* with great zeal. When it wished to fly from one plant to another it repeatedly made a mistake and flew to the flowers of *Bellis*, but having reached these it recognized its error and immediately took wing again.

In order to reconcile this short-sightedness with the great skill in flight shown by most insects, Notthast assumes that insects find a standard for judging distance in the varying distinctness of objects, resulting from their different distances—the more obscure and confused an object appears to them the further are they removed from it. It may be supposed that insects visiting flowers from considerable distances are guided to a great extent by their sense of smell. By the experiments of Forel, it has been proved, however, that insects certainly perceive flowers at a considerable distance without having recourse to the sense of smell, and that, on the other hand, blinded insects cannot recognize the place where they wish to alight. This investigator cut away the front of the head as far as the eyes, as well as the antennae (with the organs of smell) from some males of *Bombus pratorum* which were in the habit of visiting a species of *Veronica*. One of them flew as before from flower to flower, but because it was unable to feed paused only an instant at each and then took wing again. Wasps (*Polistes gallica*) mutilated in the same way behaved similarly (Kolbe, op. cit., pp. 475, 476).

The frontal ocelli which many species possess (Fig. 57 *a*) appear, as their position indicates, to come into action when the insect flies out into the clear sky, or towards a point of light, by enabling the brightness or the source of illumination to be recognized. They are not able, however, to distinguish the forms of external objects.

Focke (*Abh. natur. Ver.*, Bremen, xi, 1890) summarizes his observations on the visual capacity of flower-visiting insects in the following statements:—

1. Lepidoptera and flies are, in many cases, chiefly guided by the sense of smell to the plants they seek; in the Hymenoptera, on the other hand, smell serves only exceptionally as an indispensable aid to the discovery of nectar-producing flowers (e. g. in the lime).

2. Insects can only see very near objects distinctly. At a distance of about 10 cm. the visual impressions of bees and humble-bees are indistinct, while some Lepidoptera and flies are still more short-sighted.

3. Insects receive only confused visual impressions from objects at a greater distance. They are able, however, to distinguish differences in colour from relatively far off, provided the coloured objects are sufficiently large, and are sharply marked off from their surroundings. A brightly coloured flower, 1 cm. in diameter, is seen against the greensward by bees, humble-bees, and Lepidoptera, from a distance of 1 to 2 m. White flowers, when it is dusk, appear to be perceived from much greater distances by hawk-moths. But it remains doubtful whether the insects are not guided by their sense of locality, and by experience acquired during preceding days, to the neighbourhood of the nectar-yielding flowers.

4. The colour-sense of particular species of insects is developed to varying extents and in different ways.

We are indebted to Lord Avebury (Sir John Lubbock) for the discovery that insects are able to distinguish colours. He accustomed (Kolbe, 'Einführung,' p. 479) bees to search for honey on paper of a particular colour. He put a honey-bee to some honey on green paper, and after it had made the journey to the hive twelve times, substituted a red paper for the green paper, and placed the latter at some distance. The bee returned, however, to the honey upon the green paper. He then carefully brought back the green paper with the bee upon it to the former situation, and replaced it when the insect had flown away again by a yellow paper, again removing the green paper. The bee this time once more returned to the green paper. The same thing happened when he replaced the green paper by orange-red, white, and blue papers: the bee returning each time to the green one. The experiment was repeated on other bees with the same result.

According to Hermann Müller's numerous (2,686) experiments (Kosmos, xi, 1882, pp. 414-25) bright yellow is less agreeable to the honey-bee than any other colour. Yellowish-white and white are visited at least as readily, or even more readily than some shades of purple, but less readily than blue and violet. The blue of bee flowers is preferred to the red, or is liked equally, but, on the other hand, red in bee flowers is preferred to yellow. Next to blue, violet takes first place.

Were one to attempt the construction of a scale of bee-flower colours, the following would represent their order:—bright yellow, white, red, violet, and blue, in special shades, for some reds act like certain blues, e.g. rose-red like sky-blue and beautiful purple like cornflower-blue.

Glaring floral colours, especially brilliant yellow, do not appeal to the honey-bee, and leaf-green is less agreeable to it than the hues of bee flowers.

Hermann Müller deduced the following results with regard to colour preference in the honey-bee from often repeated experiments carried out at a later date. For each of these he used only two glass plates provided with honey, and with floral leaves of particular colours placed beneath them.—

1. Whenever a glaring colour (e.g. the yellow of *Ranunculus*, the orange of *Calendula*, the fiery-red of *Tropaeolum*, or the scarlet of *Papaver Rhoeas*, *Canna*, and so forth) lay beside a bee-flower colour for choice, the latter was much more frequently visited than the former.

2. Of all bee-flower colours bright yellow is least agreeable to the honey-bee.

3. Pale yellow and white are visited by the honey-bee at least as readily, or even more readily, than some shades of purple, but less readily than blue and violet.

4. Blue is either preferred to bee-flower red by the honey-bee, or is visited equally, according to the shades which are contrasted.

5. Pure saturated blue attracts the honey-bee even more than violet does.

6. Violet has a stronger influence on the honey-bee than any other floral colour contrasted with it, blue excepted.

The following series, therefore, gives the colours which are appreciated by the honey-bee in the order of preference—saturated blue, violet, blue, red, white and pale yellow, pure green, glaring red, and glaring yellow.

As already explained in an earlier chapter (see p. 124) the colour-sense is also particularly well developed in butterflies:—*there is certainly a remarkable correspondence as to colour between some flowers and the Lepidoptera which visit them.* Hermann Müller (Kosmos, iii, 1878, p. 418) gives the following additional examples of this:—The orange-hued Composites *Crepis aurea*, *Hieracium aurantiacum*, and *Senecio abrotanifolius*, are a veritable playground in sunny weather for butterflies of fiery-red colour (*Argynnis Aglaja*, *Polyommatus Virgaureae*, *P. hippothöe* var. *eurybia*). Hermann Müller saw the two copper butterflies (*Polyommatus*) in question and *Argynnis pales* flying repeatedly even to the bright red fruits of *Rumex*, and Blues (*Lycaena*) settling with unmistakable preference on the blue capitula of the alpine species of *Phyteuma*. He is, therefore, inclined to think that the same 'preference of butterflies for certain colours, as expressed in their own adornment, which has been acquired by sexual selection, has also determined their choice of flowers, and therefore, indirectly, the colour of lepidopterid flowers, as also the surprising resemblances existing between the odours of butterflies and those of the blossoms they pollinate.'

A case of protective resemblance described by E. Köhne (Verh. bot. Ver., Berlin, xxviii, 1886, pp. 6-7) may be appropriately given here as a final illustration of the above principle. This observer noticed, not far from Wangerin in Pomerania, a very large number of male and female brimstone butterflies (*Rhodocera Rhamni* L.) on the pale capitula of the cabbage thistle (*Cirsium oleraceum* L.). In the position of rest the butterfly held its wings vertically, so that their under-sides alone were visible, and these, especially in the rather whitish female, harmonized so remarkably with the colour of the capitulum and its involucre that when the light was bright not the slightest difference of hue could be perceived. And it must be added that the involucral bracts project to some extent above the capitulum, and that the shape of the resting butterfly, as determined by its pointed wings, obviously simulates that of the upwardly directed points of the bracts. Even the clear veining of the under-sides of the wings forcibly reminds one of that of the leaves. In fact, the form and colour of the capitula and involucre agreed so closely with those of the butterfly, when seen in the glaring sunshine, that Köhne could not distinguish with certainty, even from a very small distance, whether or no a brimstone butterfly was resting on a given capitulum, and he did not usually perceive the insect till it flew off on his approach. He regards this remarkable colour-agreement between butterfly and plant as a *mutual adaptation*. When on the wing, this butterfly, like most others, is protected from the attacks of enemies by its erratic, undecided, devious flight; if at rest it is never better protected than when it has settled on the yellowish capitulum. In places where *Cirsium oleraceum* grows, it will therefore be able to maintain itself in large numbers, and will consequently leave numerous offspring. The plant, on the other hand, is assured of many visits from the insect, and hence of amply sufficient pollination and seed-production. It too is, therefore, able to multiply to an unusual extent.

The significance of the individual groups of insects, with reference to the pollination of flowers, has already been dealt with by Hermann Müller, who has also given an exhaustive account of their structural peculiarities, so far as they are

related to this. I shall therefore, in the following account, substantially repeat the descriptions of this distinguished investigator.

A. Membrane-winged Insects (Hymenoptera).

Of insects concerned with the pollination of European flowers, these are the most important. The first place must be given to

BEES (APIDÆ),

which of all insects stand on the highest level of specialization in regard to flower pollination, and are alone capable of putting into action numerous flower-mechanisms which remain closed to all other visitors. Not only are they most skilful in the quest for flower-food, but they are also most zealous, for besides feeding upon substances derived from flowers as adults, they rear their young entirely on such food. The whole existence of bees is therefore, says Hermann Müller ('Fertilisation,' p. 46), bound up with flowers to such an extent that they by themselves present more adaptations to procuring flower-food, and considerably more with regard to pollination, than all other orders of insects, with the possible exception of Lepidoptera, put together, and have therefore brought about a large number of floral adaptations.

The *honey-bee* (Fig. 58, 5, 6) is pre-eminent among its kind as regards adaptation to pollination. With wonderful certainty it solves the problems presented

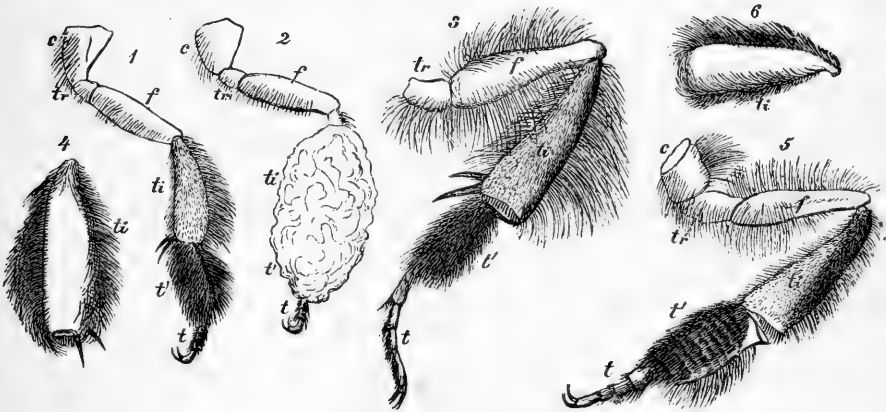


FIG. 58. *Pollen-collecting apparatus on the hind-legs of bees* (after Hermann Müller). (1) Right hind-leg of *Macropis labiata* *Pr.* ♀, seen from behind and within. (2) The same laden with pollen of *Lysimachia vulgaris*. (3) Right hind-leg of *Bombus Scrimshiranus* *K.* ♀, seen from behind and within. (4) Tibia (shin) of the same, seen from the outer side (collecting-basket). (5) Right hind-leg of the honey-bee (*Apis mellifica* *L.* ♀), seen from behind and within. (6) Tibia (shin) of the same from the outer side. *c*, coxa (hip); *tr*, trochanter; *f*, femur (thigh); *ti*, tibia (shin); *t*, tarsus (foot); *t'*, basal joint of the tarsus. Fig. (1) naturally only shows in side view the collecting-hairs of *Macropis*, which cover the outer surfaces of the tibia, and basal joint of the tarsus.

by the most involved floral mechanisms. It goes to work in a purposeful manner, as if conscious of the end in view, and confines its attention strictly to the species of flower it has selected. Its body presents the most perfect adaptations to the collection of pollen and the sucking of nectar. For gathering pollen it has a pollen-collecting apparatus on its hind-legs, and this is the most perfect arrangement of the kind in any of the 'scopulipedes,' one of the chief divisions of the bees.

It consists of stiff hairs on the tibiae, and a 'basket' (composed of bristles arranged in rows) on the basal joint of the tarsus. Among the other 'scopulipedes' (*Bombus*, *Macropis*, *Anthophora*, *Dasypoda*, *Andrena*, *Halictus*, *Sphecodes*) this collecting-apparatus is not so perfectly developed as in the honey-bee.

In the genus *Bombus* (Fig. 58, 3), for instance, the hairy investment (vide infra) of the collecting-basket is not, as in *Apis*, converted into perfectly simple, smooth, stiff bristles, placed in few rows and at tolerably equal distances, but presents a much less perfect arrangement. It consists of many irregular rows of bristles, which possess more or less distinct feathery branches. The collection of pollen (Hermann

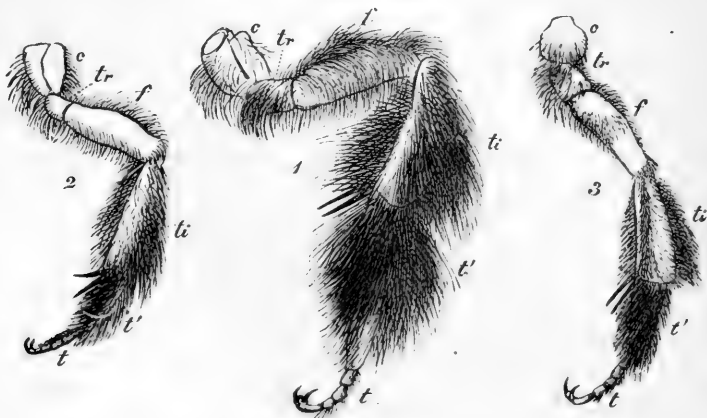


FIG. 59. *Collecting-hairs on the tibia and basal joint of the tarsus.* (1) Right hind-leg of *Dasypoda plumipes* Pz. ♀, seen from behind and within. (2) The same of *Panurgus Banksianus* K. ♀. (3) The same of *Podalirius bimaculatus* Pz. ♀ ($\times 7$). References as in Fig. 58.

Müller, 'Fertilisation,' p. 53) is confined, however, as in *Apis*, to the outer side of the hind-legs, so that the mobility of the limb is very great. The outer surface of the hind-tibiae is as smooth as a mirror, and only fenced in at the edge with a palisade of long hairs, partly erect, partly inwardly curved, so as to form the 'basket,' in which pollen moistened with honey can be heaped up far beyond the limits of the palisade¹. In this way there is not only economy of hairs and of time in the process of emptying the collecting-apparatus, but the tarsal brushes of the hind-legs can be used freely and without impediment.

In *Macropis* (Fig. 58, 1) this is not the case, for the tarsal brushes are surrounded with thick balls of moistened pollen, as well as the tibiae, which are clothed with relatively short collecting-hairs.

¹ According to Hindenberg (Monatl. Mitt. naturw. Ver., Frankfurt a. O., vii, 1889) pollen-masses on the leg of the honey-bee are, on an average, 3.5 mm. in length, and 2 mm. in breadth. Should they consist of the pollen of *Centaurea Scabiosa*, there would be 125,000 pollen-grains in each of them. The brushes on the inner side of the basal tarsal joint of the hind-leg of the bee are made up of nine rows of smooth, half-erect bristles, of which there are twenty-four in the longest row. The distance of the bristles from one another is 0.04 mm., and therefore corresponds to the size of the pollen-grains mostly collected. Investigation of the pollen-balls of a honey-bee returning from the country, shows that they contain pollen-grains of only a single species of plant.

In the species of the above-named three genera, the habit exists of wetting the pollen with honey before heaping it up in the collecting-apparatus, thus making it into a coherent mass, which does not need to be entirely enclosed by collecting-hairs. This mass can easily be taken out of the collecting-apparatus and at once used as larval food. The pollen-apparatus of the hind-legs is therefore extremely perfect and permits considerable economy of collecting-hairs, and also much saving of time in emptying the collecting-apparatus and preparing the larval food. In the genera *Eucera*, *Anthophora*, *Dasypoda*, and *Panurgus*, the collecting-hairs are limited as in the previous genera to the tibiae and basal joints of the tarsus, so that here too a rapid and convenient removal of the collected pollen is possible. Indeed *Eucera* and *Anthophora* already possess an arrangement resembling the collecting-apparatus of *Bombus*, for a greater broadening of the pollen-receiving tibia and basal tarsal joint has rendered possible a relatively small development of hairs, which interfere with flying and creeping movements. In *Panurgus*, the hairs on the tibia and proximal tarsal joint, which represent the collecting-apparatus, are considerably longer and therefore more in the way than in *Eucera* and *Anthophora*, but even here they are entirely confined to these regions. In *Dasypoda*, on the other hand, not only are the collecting-hairs of the tibia extraordinarily long, so that the movements of these bees are slow and almost clumsy compared with those belonging to the genera already mentioned, but the thigh, the trochanter, and coxa are also beset with long, thick hairs, so that these parts share in the collecting of pollen, though in a lesser degree. *Dasypoda hirtipes* has such long feathery collecting-hairs on the coxae, tibiae, and the greatly elongated basal tarsal joints of the hind-legs, that it is able to heap upon them immense balls of pollen, which may be half the size of the abdomen. Sprengel ('Entd. Geh.' p. 370) observed this bee on *Hypochoeris radicata*. 'At noon, during beautiful weather, I noticed a bee on this plant, with such large balls of pollen on its hind-legs that I was amazed. They were not much smaller than the entire body of the insect, and gave it the appearance of a heavily-laden pack-horse. Yet the bee could fly with its burden at a great rate, and was not yet contented with the provision it had collected, but flew from one flower-head to another to increase its load.'

Hermann Müller (Verh. nathist. Ver., Bonn, xli, 1868, pp. 1-62) states that a single load of pollen, such as a female of *Dasypoda hirtipes* carries to her nest, weighs about half as much as her own body. Five or six such loads, after they have been moistened with honey, are made by the bee into a ball weighing 0.23-0.36 gr., and this is entirely consumed by the larva that develops upon it.

The species of *Panurgus* with their highly developed collecting-apparatus visit, almost exclusively, yellow Composites of the group Cichoraceae, chiefly limiting their activity to the collection of pollen. When on a capitulum they often turn over on their sides or roll about, and are almost hidden among the florets.

As regards specialization in relation to flowers these four genera are considerably lower in the scale than *Apis*, *Bombus*, and *Macropis*, for they are not in the habit of moistening the pollen before loading themselves with it, so as to form a coherent mass which can be taken from the collecting-apparatus in the shortest possible time (cf. p. 146).

The genera *Anthrena*, *Halictus*, and *Prosopis* are at a much lower stage in respect of adaptation to flower-food. In many species of the two first-named genera

the hind-legs are thickly covered with hair from the tibia to the coxa. Even the metathorax is sometimes provided with two well-developed tufts of hair, under which considerable quantities of pollen can be accumulated (H. Müller, 'Fertilisation,' p. 51). Compared with the species of *Sphecodes*, those of *Halictus* and *Anthrena* have an advantage in that their basal tarsal joints are considerably broader, and the tarsal brushes are consequently more effective. These bees will therefore use exclusively or chiefly as larval food the pollen that is collected by the hairy covering of the hind-legs, whilst for the species of *Sphecodes* this method of collection is subsidiary.

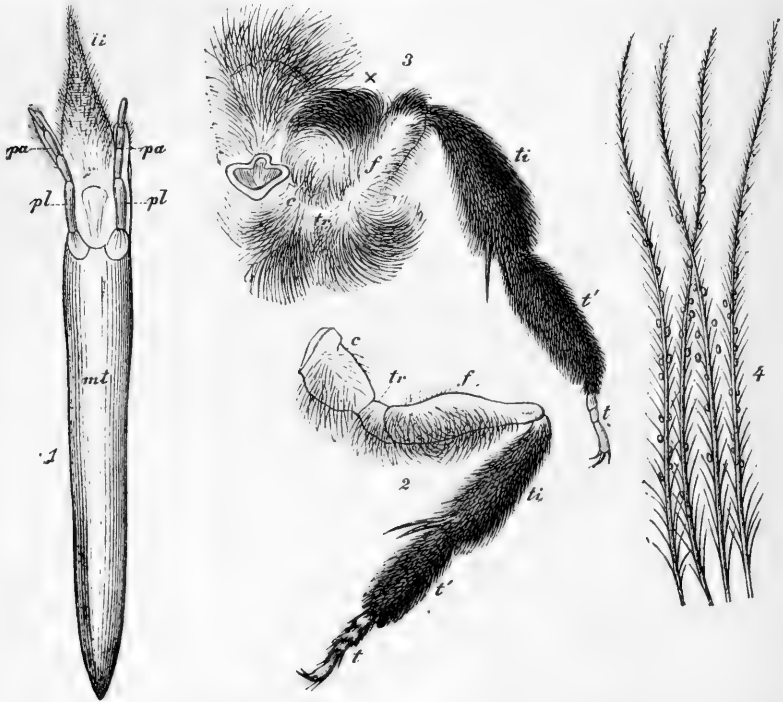


FIG. 60. *Halictus* and *Anthrena* (after Hermann Müller). (1) Labium (lower lip) of *Halictus quadricinctus* F. ♀: *mt*, mentum (chin); *li*, ligula (tongue); *pa*, paraglossae (accessory tongues); *pl*, labial palp. (2) Right hind-leg of the same bee. (3) Metathorax and right hind-leg of *Anthrena ovina* Klg. ♀; *x*, right tuft of hair on the metathorax. Other references in (2) and (3) as in Fig. 58. (4) Single hairs from the body of an *Anthrena ovina* Klg. ♀, captured upon a flowering willow. To the feathery branches of these hairs numerous pollen-grains are sticking.

As in all the three above-named genera the entire body is hairy, it follows that the bees in visiting numerous flowers cover themselves with pollen, which they subsequently remove with the tarsal brushes, so that the quantity heaped up on the special collecting-hairs is considerably augmented, especially as the hairs are mostly feathery. In *Sphecodes* the hair-covering of the body is very scanty. Only the legs are well covered, especially the outer sides of the posterior tibiae. The brushes on the inner side of the basal tarsal joints are somewhat better developed than in the genus *Prosopis*, a bee which is at the lowest stage of adaptation. The species of the latter have an almost naked body, and the small basal tarsal joints possess but a feebly-developed covering of hair. Pollen, however, often clings to these bees,

especially to their hind-legs, and they possess feebly-developed tarsal brushes, which can be used not only to clean the body, but also to collect pollen which has adhered to any part of it. The genus *Prosopis*, therefore, is on the lowest level among bees, and belongs to them only because of the way it feeds its young. They fill their brood-chambers (which are coated by means of their broad tongue with hardened slime) with a mixture of regurgitated honey and pollen, and this serves as nourishment for the larva when it escapes from the egg (Hermann Müller, 'Fertilisation,' p. 47). The same method of nourishing the young also occurs in *Sphecodes*, but here the larvae are fed not only on regurgitated honey, but also on pollen that has adhered to the hairy covering of the bee's body. The latter merely supplementary method of collecting pollen as larval food by means of the body-hairs becomes the exclusive or at any rate the chief one ('Fertilisation,' p. 51).

In contrast to the above-described 'scopolipedes' are the 'dasygastres,' to which the species of the genera *Anthidium*, *Chalicodoma* (now united with *Megachile*), *Chelostoma*, *Diphysis*, *Heriades*, *Megachile*, and *Osmia* belong. In this second main group of bees there are no marked differences as regards the formation of the pollen-collecting apparatus, which is pretty much the same in all the genera.



FIG. 61. *Sphecodes* (after Hermann Müller). Right hind-leg of *Sph. gibbus* L. ♀, seen from behind: *c*, coxa (hip); *tr*, trochanter; *f*, femur (thigh); *ti*, tibia (shin); *t*, basal joint of the tarsus; *t'*, tarsus (foot).

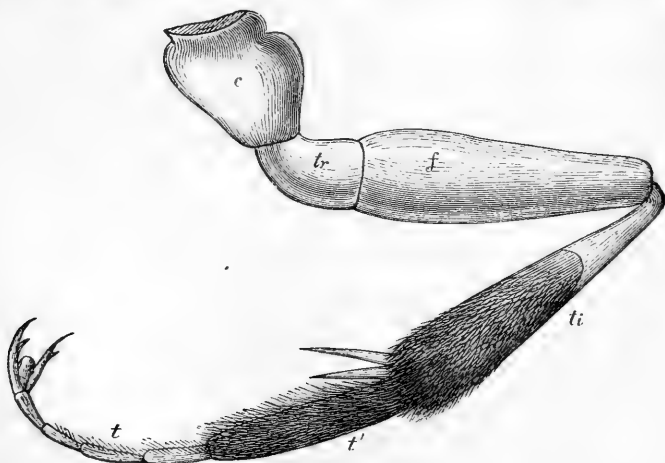


FIG. 62. Right hind-leg of *Prosopis variegata*, F. ♀, seen from behind (after Hermann Müller). *c*, coxa (thigh); *tr*, trochanter; *f*, femur (thigh); *ti*, tibia (shin); *t*, joints of the tarsus (foot); *t'*, basal joint of the tarsus.

It will therefore be sufficient to consider one only, and here again I shall follow Hermann Müller ('Fertilisation,' p. 34), whose account is somewhat as follows:—

The whole or nearly the whole ventral surface of the abdomen is covered with a single brush of stiff bristles inclined backwards, and which vary greatly in length, closeness, and colour in different species, but are always simple and smooth, without

trace of feathery branching. The abdominal collecting-apparatus of one division of the bee family stands in sharp contrast to the collecting-apparatus developed on the hind-legs of the other division, not only in the structure of its hairs, but also in the way it is used. The pollen-collecting apparatus of the latter consists of a forest of feathery hairs, into which the tarsal brushes (formed of simple stiff bristles) sweep the pollen they have scraped off. In the present group, on the other hand, the pollen-collecting apparatus is a large brush of simple rigid bristles, and this itself sweeps up the pollen. That this difference of function, to which the difference of structure points, actually exists, is thoroughly confirmed by observing the visits which the dasygastres make to flowers. For more than nine-tenths of the flowers visited by bees with abdominal brushes are such as are adapted to dust the ventral surface of the bee with pollen (*Echium*, *Papilionaceae*, *Compositae*, and so forth), so that the ventral collecting-apparatus is frequently completely filled with pollen without any help from the tarsal brushes. On the heads of *Compositae*, for example, dasygastres may be seen rapidly thrusting their tongues into one floret after another for the purpose of getting nectar, meanwhile turning the body half or entirely round, so that the pollen lying loose on the surface of the head is forced between the hairs of the abdominal brush. This is quite full after a few heads have been visited. In this

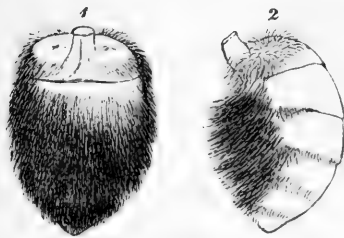


FIG. 63. *Abdominal collecting-apparatus* (after Herm. Müller). (1) Abdomen of *Osmia spinulosa* K., seen from below. (2) Side view of the same ($\times 7$).

way Hermann Müller very frequently saw, for example, *Megachile lagopoda* L. upon *Onopordon Acanthium*, and *Osmia spinulosa* K. upon *Carduus acanthoides*. More rarely bees of this group gather pollen on flowers which deposit it on their backs. In such cases they use their tarsal brushes to remove pollen that remains sticking among the feathery hairs that cover their bodies, and bring it to the abdominal brush. Hermann Müller saw, for example, *Anthidium manicatum* L. behaving in this way on the flowers of *Ballota nigra*.

The abdominal collecting-apparatus is similarly formed in bees belonging to different genera, while, as shown above, the collecting-apparatus on the hind-legs exhibits gradual specialization, step by step, from *Prosopis* to *Apis*. It is also possible to recognize a series of adaptations in the mouth-parts having reference to getting nectar from flowers. Hermann Müller describes these ('Fertilisation,' pp. 48-64) somewhat as follows:—

When at rest (Fig. 64, 1) the lower mouth-parts, i.e. maxillae and labium (under lip), are withdrawn in *Prosopis* into a cavity on the under-side of the head, which they exactly fill, and this is effected by means of the folding together of stiff chitinous parts, which are united by movable joints. The two basal pieces or cardines of the maxillae (Fig. 64, 4, *cc*) are jointed into two sockets at the sides of the cavity under the head, in such a way that they can rotate either forwards or backwards. When at rest they are folded back, drawing with them the stipites (stems) of the maxillae (Fig. 64, 1, 2, 3, 4, *st*), which are movably articulated to their distal ends, and also the mentum (*mt*), which is fastened between them, the result being that they are completely covered by these structures. The laciniae of

the maxillae (*la*), the maxillary palps (*pm*), and the labial palps (*pl*) are also turned downwards and backwards, and the mandibles (*md*) are brought together over the bases of these parts, at the same time overlapping the downwardly folded labrum (Fig. 64, 2, *lbr*) and the retracted ligula (*li*). In the state of rest the mandibles alone retain their position unchanged, and are able, without alteration in the position of any other mouth-part, to open and close like the sides of a pair of tongs, i.e. they can bite. When they separate (Fig. 64, 2), the labrum (*lbr*), ligula (*li*), the bases of the backwardly turned laciniae (Fig. 64, 2*b*, *la*), the maxillary palps, and the labial palps become visible.

Should the bee wish to cease biting and begin to suck nectar, it extends the laciniae, maxillary palps, and labial palps forwards, and spreads out the ligula

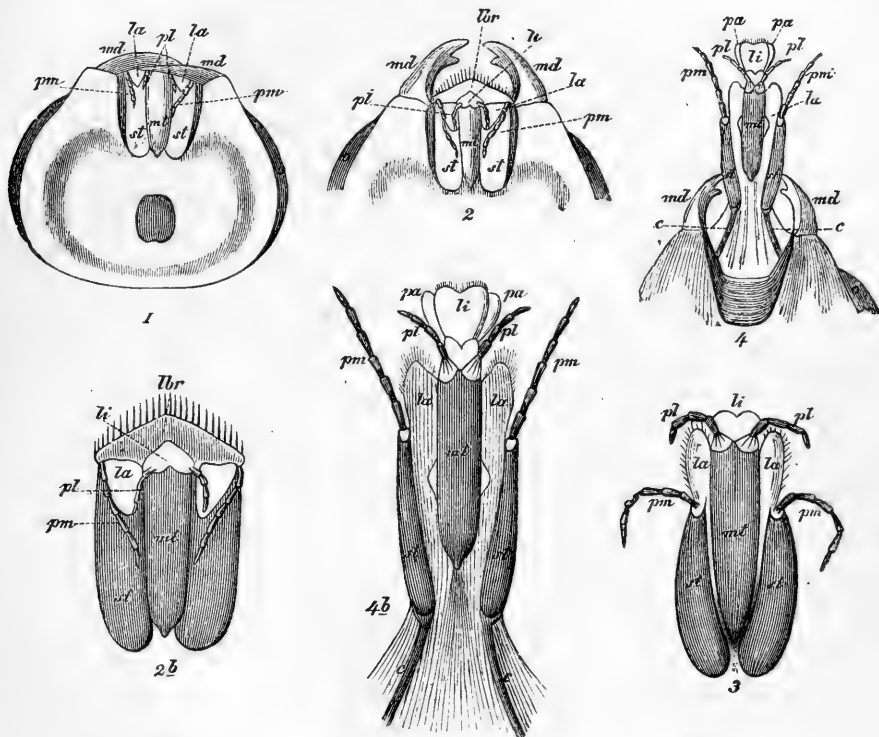


FIG. 64. *Mouth-parts of Prosopis* (after Herm. Müller). (1) Head with mouth-parts completely apposed, seen from below. (2) Anterior parts of the same with the mandibles separated, and the labrum turned up. (2*b*) Mouth-parts in the same position, more highly magnified. (3) Mouth-parts, after the elevation of the maxillae and the maxillary and labial palps, and with the ligula partly extended; magnified as in (2*b*). (4) Ventral view of the front part of the head with mouth-parts fully extended; magnification as in (1) and (2). (4*b*) The completely extended mouth-parts; magnified as in (2*b*) and (3). *lbr*, labrum (upper lip); *md*, mandible (upper jaw); *c*, cardo (basal joint of the maxilla or lower jaw); *st*, stipes (stem of the maxilla); *la*, lacinia (blade of the maxilla); *pm*, palpus maxillaris (maxillary palp); *mf*, mentum (chin); *li*, ligula (tongue); *pa*, paraglossae (accessory tongues); *pl*, palpus labialis (labial palp); *o*, eye.

(Fig. 64, 3). It then rotates the cardines of the maxillae (Fig. 64, 4, *cc*) to the front, and this protrudes the maxillae and labium (mentum and ligula) about twice the length of the cardines, so that the ligula can be inserted into nectar receptacles which are not too narrow or too deep.

The power of folding up the lower mouth-parts into the cavity of the head for biting, and of unfolding and protruding these parts for sucking, exists in Digging Wasps (Fossores) much as in *Prosopis*. Although these insects are sometimes found on flowers, most of them store up other insects in their holes in the earth or in walls for the use of their larvae. *Prosopis*, therefore, is not specially adapted to flower-food.

Hermann Müller ('Fertilisation,' p. 49) goes on to say that *Sphecodes*, *Halictus*, and *Andrena* (genera related to *Sphecodes*, but much more specialized) are considerably higher in the scale than *Prosopis*, in regard to adaptation to flower-food. In all three the tongue is still moderately short (Fig. 65, 4, *li*; Fig. 60, 1), but is able to

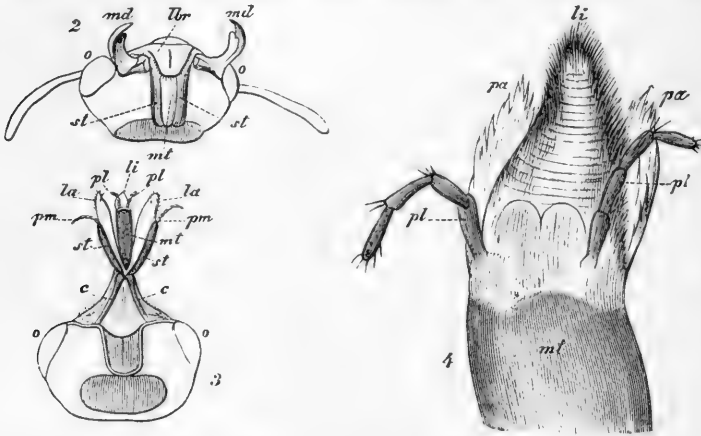


FIG. 65. *Sphecodes* (after Herm. Müller). (2) Head of *Sphecodes*, with mandibles opened, but lower mouth-parts folded and hidden under the labrum; seen from in front and below. (3) The same, after removal of the mandibles and of the labrum, with unfolded and protruded lower mouth-parts. (4) End of labium more highly magnified, seen from above. References as in Fig. 64.

insert itself into somewhat deeper nectar-receptacles, not so much on account of its own length as by the greater elongation of the mentum and cardines. The ligula (unlike that of *Prosopis*) is here pointed, more or less hairy, and marked by fine transverse lines at its tip (Fig. 65, 4). In some species of *Andrena* and *Halictus* it has assumed a much narrower and more slender form, for it is here less concerned with nest-building, as the bees in question smooth the walls of their brood-chambers (which are mostly underground) with only a very little slime.

In these four genera, increased protrusibility of the ligula is therefore attained by a lengthening of the mentum and cardines. Owing to the length of the head, beneath which these parts must be withdrawn when the mandibles are used, this extension is naturally limited. Hence the only further adaptation enabling more deeply seated nectar to be reached is by elongation and increased development of the ligula itself, with the extension of the connecting piece between the mentum and cardines.

We therefore find, among the higher forms of both scopolipides and dasygastres ('Fertilisation,' pp. 56 et seq.), that the ligula, which in bees little adapted to flower-food is much shorter than the mentum and retractile into it, may be many times the length of the mentum. At the same time, the transverse striations (absent in

Prosopis, feeble in *Sphecodes*, more clearly visible in *Halictus*) are represented by prominent transverse rings over the greater part of the worm-like ligula. The hairs on the ligula, which scarcely present any definite arrangement in the lowest stages mentioned, form regular whorls on each transverse ring that can be erected and forwardly depressed. And, lastly, the movable membrane connecting mentum and cardines is extended and supported by chitinous bars, in such a way that when these fold together the mentum is retracted between the stipites as far as the ends of the cardines, while when the chitinous bars unfold it is protruded for their full length.

Certain modifications of the maxillae are inseparably connected with these specializations of the labium, so that the same successive stages can be recognized in both groups of bees. As soon as the ligula is so far lengthened that it can no longer be retracted into the anterior hollow of the mentum, it is folded up downwards and backwards when not in use, and both in the retracted and protruded condition is sheltered between the laciniae so as to be protected from injury during nest-building and the process of penetrating into nectar-receptacles. The laciniae having come to serve as a sheath for the elongating ligula must therefore extend in the same proportion. The labial palps elongate similarly, in order that they may continue to act as tactile organs, and when the ligula is not too long this is also the case with the maxillary palps. The latter, however, are soon outstripped by the continually elongating laciniae, labial palps, and ligula, and ultimately degenerate, while the laciniae and labial palps keep pace with the ligula even to its highest degree of elongation. The difference between the changes undergone by the maxillary and labial palps, which originally had the same function, is explained as follows. With increasing elongation of the ligula, the laciniae become modified to form a sheath, closely enveloping the ligula, and protecting it from injury, both when retracted and also while being inserted into flower-tubes. During the sucking of nectar the laciniae also assume the rôle of a suction-tube, in which the nectar probably passes to the mouth by the successive erection of the whorls of hairs on the ligula, from the tip upwards. The labial palps are also pressed into the service of this curious suctorial apparatus, by the flattening of two or three of their basal joints, so as to help the laciniae in the close sheathing of the ligula, the last joint or two, however, retaining the original tactile function. This explains the elongation of the basal joints of the labial palps, which keep pace with the growth of the ligula and laciniae. They become long, thin, chitinous plates enveloping the ligula, while the still tactile end-joints retain their original form and shortness, as well as their free external position. The six-jointed maxillary palps, on the other hand, having been outstripped by the elongating laciniae, are handed down merely as useless appendages, and therefore present all stages of degeneration from six joints to none at all.

A final increase in the length of the ligula, beyond that of the structures which ensheath it, is attained by making the proximal part of this worm-shaped organ (which is fused with the paraglossae) coil twice round when retracted into the hollow end of the mentum. The ligula, therefore, when drawn back, reaches just to the end of its sheath, but when fully protruded projects to a distance about equal to the length of the sheath. The sucking-apparatus of bees, greatly elongated in the way described, is also adapted for boring juicy tissues by the sharpening of the laciniae,

while the development of a membranous lappet on the tip of the ligula presumably renders it possible to lick up flat layers of nectar.

Just as the pollen-collecting apparatus has reached its highest degree of development in *Apis* and *Bombus*, so also has the mouth of these bees become best adapted for riffling the nectar of flowers. It is therefore intelligible that bees belonging to these two genera play a far more important part than any other insects in the pollination of our indigenous flowers.

Grabert ('*Werkzeuge der Tiere*,' II, p. 213) rightly says that what makes the humble-bee proboscis so marvellous is not so much its individual parts, as the way in which these are united into a complete whole. Considered as a mechanism the proboscis is a tube composed of several long splints (and therefore dilatable) within which the actual receptive organ, i.e. the ligula, moves up and down. This tube or sheath of the ligula consists of the two-grooved laciniae above, and the labial palps below. At the base of the proboscis, the cavity of this sheath passes into a canal formed by two gutter-like basal pieces of the maxillae and labium, and is finally connected with a curious pumping-apparatus situated within the cranial capsule. The suctorial proboscis of the humble-bee, and Hymenoptera generally, is interesting to us not only because it is so constructed that it can be widened and narrowed, but also because, by means of a highly specialized mechanical arrangement, it can be closed like a pocket-knife.

Hermann Müller ('*Fertilisation*,' pp. 58-64) gives an exhaustive description of the proboscis of bees and other Hymenoptera, with a thorough account of the functions of its various parts. When the mouth-parts of *Apis* and *Bombus* are fully extended and artificially separated (Fig. 66, 1 and 2), it seems at first sight hardly possible that a suctorial apparatus so large and complex, which is occasionally several times as long as the head, and in certain species even exceeds the body in length, can be completely received into a cavity below the head¹, as is the case with the short proboscis of the less specialized bees. Yet this takes place with great ease and certainty by means of the four folding movements already mentioned. We must now consider the relation of these movements to the diverse activities of the proboscis.

1. When the bee is sucking nectar which is only just accessible, all the movable joints of its suctorial apparatus—cardines, the chitinous retractors at the base of the mentum, laciniae, labial palps, and ligula—are fully extended as in Fig. 66, except that the two proximal joints of the labial palps are closely applied to the ligula below, and the laciniae to the mentum and hinder part of the ligula above. But as soon as the whorl of hair at the tip of the ligula (which is extended as far as possible, and sunk to the bottom of the flower-tube) is wet with nectar, the bee by rotating the retractors (Fig. 67, 2) draws back the mentum, and with it the ligula, so far that the laciniae reach as far forward as the labial palps (to the point *u* in Fig. 66); and now laciniae and labial palps together, lying close upon the ligula and overlapping it with

¹ It is only in the case of exotic bees (e.g. *Anthophora fulvifrons* and *Euglossa* in Brazil) that the proboscis is so long that even repeated folding is inadequate to conceal it on the under-side of the head. In such cases the protruding part lies on the ventral surface of the body along the middle line, and in *Euglossa* even reaches to the end of the abdomen.

their edges, form a tube out of which only the part *uv* of the ligula protrudes (Fig. 67). But almost simultaneously with these movements, the bee retracts the basal part of the ligula into the hollow end of the mentum, and so draws the tip of the ligula, which is wet with nectar, into the tube, where the sweet liquid is passed on by the rapid successive erection of the whorls of hair from the tip towards the base of the ligula, while the simultaneous expansion of an internal cavity in connection with the mouth (indicated externally by a swelling of the abdomen) sucks it in. The process of sucking as described in the humble-bee can readily be detected by noting the expansion and contraction of the abdomen, so that it is easy to see whether a flower which the bee is beginning to suck has already been drained of nectar or not. (Cf. also my remarks on the visit of *Anthophora pilipes* F. (= *Podalirius acervorum* L.) to *Lamium purpureum* L., p. 166.)

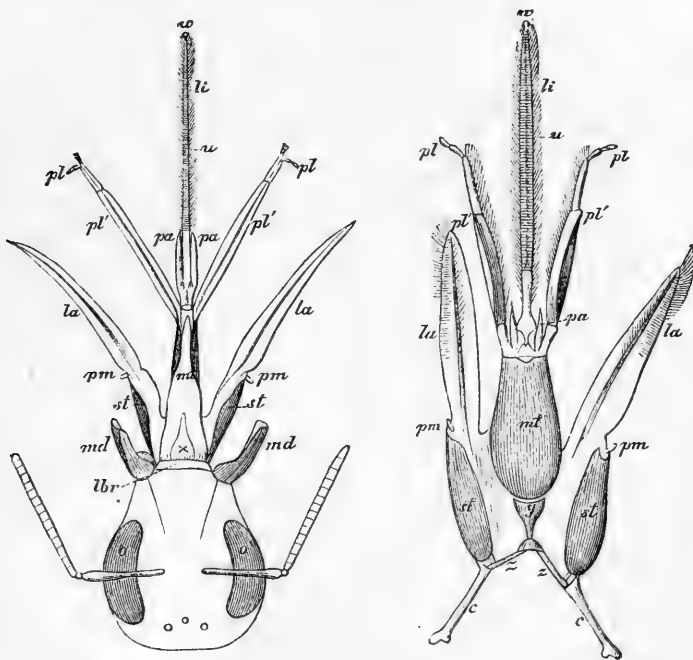


FIG. 66. *Head of humble-bee* (after Herm. Müller). (1) Head of *Bombus agrorum* F. ♀, with completely extended and widely separated mouth-parts; seen from above ($\times 5$). (2) Mouth-parts of the honey-bee in the same condition; seen from below ($\times 12$). *pl'*, The two basal joints of the labial palps, which are modified to form part of the ligular sheath; *uv*, the membranous lappets at the tip of the ligula; *x*, the piece which covers the mouth-opening, which lies between *md* and *x* (epipharynx, Westwood); *y*, submentum, the chitinous piece which lies at the base of the mentum, and continues it backwards (fulcrum, Kirby); *zz*, retractors, chitinous pieces which unite the submentum with the ends of the cardines, *cc*, and, as they revolve backwards round the ends of the cardines, retract the mentum and all its appendages (Kirby calls *zz* cardines, and *cc* lora).

‘The sucking of nectar,’ says Hermann Müller (‘Wechselbeziehungen,’ pp. 29, 30), ‘is prejudiced to an unknown extent by an imperfection in the adaptation, i.e. the character of the nectar can only be recognized after the entire space between the hairy ligula and its sheath has been filled with fluid, and this has risen as far as the taste-organs. Should it then appear to the bee that the nectar is not agreeable, sucking may cease, but this will not get rid of the layer adhering to the whorls of

hair, which may even spoil the flavour of the nectar next tasted. But by examining the ligula of a highly specialized bee under a high power of the microscope, a special arrangement by which this imperfection is obviated will easily be recognized. In less specialized bees the whole length of the tongue is supported by a massive chitinous rod; but in more specialized bees this rod is converted into a capillary tube, which opens into the hollow of the spoon-shaped lappet at the tip of the ligula. As soon as this 'spoon' is immersed in nectar, part of it rises in the capillary tube to the base of the ligula and to the taste-organs. Should the nectar, when tasted, prove disagreeable to the bee, it need not even begin to suck, and can easily expel the minute quantity of liquid that fills the tube.' (Cf. O. J. B. Wolf, 'Das Riechorgan der Biene,' 1874.)

Fig. 67 represents the head of a humble-bee in the suctorial position, with the proboscis half extended. If now, from this position, the base of the ligula is

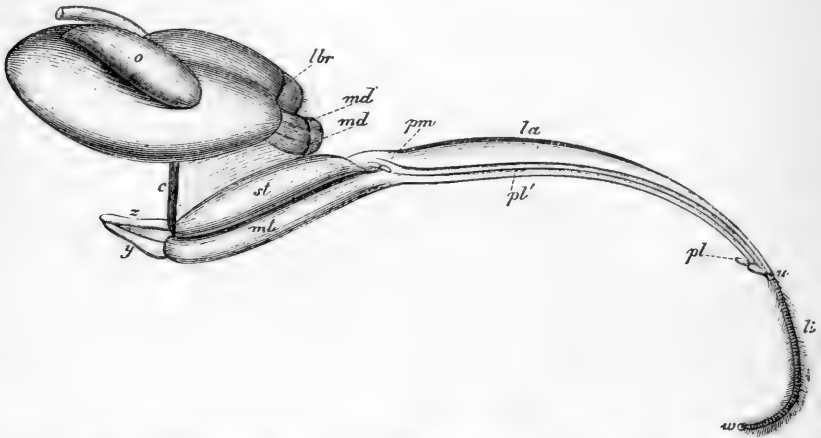


FIG. 67. Head of *Bombus hortorum*, L. ♀, with proboscis half extended; seen from the side (after Herm. Müller). (× 7.) References as in Fig. 66.

retracted into the hollow end of the mentum (as shown in Fig. 68), its end (*uw*) is drawn back saturated with nectar into the suctorial tube. If the cardines (Fig. 67, *c*), now turned vertically downwards, are rotated backwards, the base of the suctorial tube (at *pm*) will be drawn back to the opening of the mouth (between the labrum and the bases of the mandibles, and by a simultaneous sucking action of the sides of the body, and pressure of the erectile whorls of hair, the nectar is quickly carried from the tip of the ligula into the mouth¹.

¹ Hermann Müller thinks he can conclude with certainty that the whorls of hair have the function described above from experiments he made on chloroformed bees and humble-bees. In these, sometimes, if the tip of the ligula was dipped in syrup before complete loss of consciousness, the suctorial movements were induced so slowly that their separate stages could be clearly distinguished. They were as described above. What went on between the chitinous plates of the laciniae and labial palps was of course invisible, but when these parts were drawn aside, after the tip of the ligula had been moistened with syrup, a successive erection of the whorls from the tip to the base could sometimes be clearly seen. The fact that the basal part of the ligula, which is retracted into the hollow of the mentum, is free from whorls of hair is in accordance with this interpretation. [But in the English translation of Müller's book (p. 61), which incorporates more recent observations of

If the cardines (*c*) now rotate forwards again, the entire suctorial apparatus is carried forwards by twice the length of these structures. The retractors (*z*) next rotate forwards, and a further advance of twice their length is given to the mentum (*mt*) with its appendages (labial palps and ligula), while the maxillae remain in their place, and their laciniae enclose only the mentum and posterior part of the ligula. Finally, the basal part of the ligula, contained in the hollow end of the mentum, is protruded and its tip attains the maximum extension (e.g. in *Bombus hortorum*, 20 to 21 mm. beyond the mouth) and dips again into the nectar at the base of the flower-tube.

In flowers rich in nectar, a humble-bee may be seen to perform the act of sucking four or five, or sometimes even eight or ten times, the tip of the ligula being apparently dipped into the nectar, drawn back into its sheath, and the sheath drawn up to the mouth, for the same number of times.

2. To reach honey which is less deeply situated the bee need not rotate the retractors forwards. They remain directed backwards, so that the ligula is constantly ensheathed by the lacinia and labial palps, only its base moving in and out, so that, alternately, its tip wet with nectar is retracted into the suctorial tube, and after discharging its load is again protruded.

3. When the bee flies from flower to flower in search of nectar, it carries the suctorial organ ('proboscis') extended, so as to introduce it, while in the act of alighting, into the opening of a flower; but the ligula is completely concealed between the laciniae and the labial palps, so that the delicate whorls of hair are protected during the act of insertion into a flower-tube, while at the same time the terminal joints of the labial palps are able to perform their tactile function. In flying from flower to flower the base of the ligula is therefore contained within the hollow end of the mentum, and the retractors are directed backwards, while the cardines may be directed vertically downwards (Fig. 67), or forwards (Fig. 66, 2), or backwards, according to the depth of the flower which the bee has in view.

4. The mouth-parts must assume exactly the same position when the bee bores into delicate tissues with the sharp points of its laciniae, whether to get at the sap (as, for example, during visits to our meadow orchids, which do not secrete free nectar) or to suck deeply seated nectar through the hole, as in the case of *Bombus terrester*, when it visits meadow clover and many other long-tubed flowers.

5. In collecting pollen, the honey-bee and humble-bee use their mouth-parts in two different ways to moisten it, according as it is the adherent pollen of entomophilous flowers, or the loose and easily scattered pollen of anemophilous flowers. In the former case (e.g. when the honey-bee collects pollen on willow catkins) the suctorial apparatus is completely folded downwards (as in Fig. 69), and the bee brings its mouth (which lies between the labrum and the base of the mandibles)

the author, the following remarks are added to the footnote:—'At the same time, special muscles for the erection of the whorls are not present; and therefore my explanation becomes unsatisfactory. In several Brazilian bees, my brother, Fritz Müller, has found that the hairs of the tongue are transformed into stalked scales, which seem hardly fitted to drive the honey mouthwards by erection. In an undescribed azure-blue *Euglossa*, the imbricated scales seem to form a tube round the tip of the tongue, so that here suction may perhaps go on without the tip of the tongue being withdrawn into the sheath formed by the laminae [laciniae] and labial palps.'—Tr.]

close over the pollen. It then ejects a little honey on the pollen, takes it up by means of the tarsal brushes, and places it in the baskets on the tibiae of the hind-legs. The mandibles are often used to loosen the pollen before it is moistened with honey. In the case of anemophilous flowers (observed and described in *Plantago lanceolata* by Hermann Müller) the bee, hovering before the flower, ejects a little honey upon the stamens from its suctorial tube, which is fully extended, but completely sheathes the ligula. Here, therefore, as when flying to suck flowers or when boring into soft tissues, the base of the ligula is contained within the hollow end of the mentum, and the retractors are directed backwards. Since honey-bees and humble-bees when visiting entomophilous flowers extend the proboscis to suck nectar and fold it up to collect pollen, while on nectarless anemophilous flowers they obviously only gather pollen, it follows that they are never able to suck nectar and collect pollen

simultaneously. They must always do first one, and then the other, and since the pollen has to be moistened with honey, the act of sucking must always be the first.

On the other hand, all bees that gather dry pollen among a dense growth of feathery collecting-hairs are able, so far as the structure of the flower permits, to accumulate pollen and suck nectar at the same time, and they perform the latter action in exactly the same way as honey-bees and humble-bees. It is obvious that bees with an abdominal collecting-apparatus can most easily perform

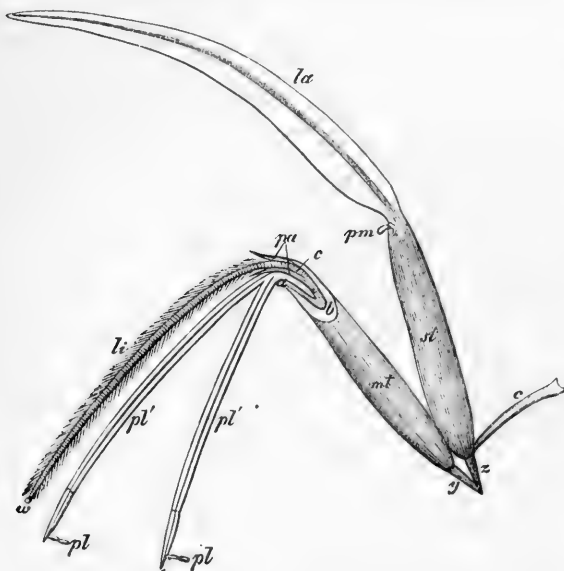


FIG. 68. Suctorial apparatus of *Bombus sylvarum*, L., half folded up; seen from the side (after Herm. Müller). The outer wall of the hollow tip of the mentum is broken away to show the involution of the proximal part of the ligula, *abc*: *a*, base of the ligula; *b*, angle of the fold; *abc*, part of ligula folded into the hollow mentum. Other references as in Fig. 64.

both acts simultaneously on flowers which present their pollen from below.

6. In order, lastly, to bring the mouth-parts to a resting position, or to use the mandibles, the bee brings into action simultaneously all the four folding movements of which its proboscis is capable. It draws back the base of the ligula into the hollow end of the mentum (as in Fig. 68), folds the ligula, together with the ensheathing laciniae and labial palps, downwards and backwards (Fig. 68 shows the beginning of this action), rotates the retractors (*z*) backwards (half completed in Fig. 68), and rotates the cardines (*c*) (which in Fig. 68 are still directed obliquely forward) backwards upon their bases. The entire suctorial apparatus is thus folded up and retracted into the cavity in the under-side of the head, which it completely fills (Fig. 69, 1).

When the honey-bees and humble-bees, the complex suctorial apparatus of which, in its various activities, has just been described after Hermann Müller's account, are declared by this investigator to be the most important of all insects in the pollination of our native flowers, his assertion, of course, only applies to those individuals concerned in the care of the young, i.e. the workers among honey-bees, and the females and workers among the humble-bees.

In all bees which provide for their own young, the males, H. Müller goes on to say, are of much less use in pollinating plants than the females, as they only look after their own maintenance, and consequently neither collect pollen, nor visit flowers very diligently. Yet, in all species in which a more or less thick coat of feathery hairs has become developed upon the bodies of the females, this is also present in the males, so that they, since they visit flowers, transfer pollen as well as the female. It is otherwise with most of those bees which have acquired the habit of laying their eggs in the nests of other bees already stored with larval food, instead of nourishing their brood on flower-food they have themselves collected.

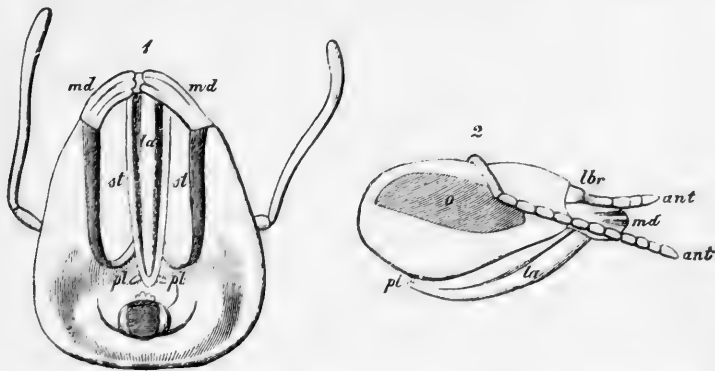


FIG. 69. Mouth-parts of a humble-bee (*Bombus hortorum*, L., ♀), retracted (after Herm. Müller). (1) Head seen from below. (2) The same seen from the side (with proboscis directed somewhat downwards). *ant*, antennae. Other references as in Fig. 64.

Some of these 'cuckoo-bees' (*Apathus*, or *Psithyrus*) have almost the same development of hairs as their parent-stock (*Bombus*), from which H. Müller concludes that they acquired the habit of brood-parasitism in comparatively recent times. Others again, in which the transition to this mode of life took place very long ago (*Coelioxys*, *Epeolus*, *Nomada*, *Stelis*), have in the course of time almost completely lost the coat of hairs that was useful to their ancestors but would be useless to them. They retain in full perfection, however, the ancestral suctorial apparatus, of which they make constant use in procuring their own food. Males and females of these 'cuckoo-bees' thus plunder flowers of their nectar, like the males of hairy bees, without being of corresponding advantage to the flowers in the transfer of pollen, for only very little of this adheres to their naked or almost naked chitinous investment.

To the admirable account that Hermann Müller has given of the structure and functions of the mouth-parts of bees, a few observations remain to be added regarding the actual length of the proboscis in various species, and the visits made to flowers by the members of various groups. It is obvious that there must be an intimate connection between the length of the proboscis of insects and the

concealment of nectar in the flowers that they prefer to visit. Some of the relative facts are as follows:—

		<i>Length of Proboscis.</i>	
Species of <i>Prosopis</i>		1-1.25 mm.	
"	<i>Halictus</i>	1.5-6	"
"	<i>Anthrena</i>	2-7	"
"	<i>Apis mellifica</i>	6	"
"	<i>Eucera longicornis</i>	10-12	"
"	<i>Anthophora retusa</i> <i>L.</i>	15-17	"
"	" <i>acervorum</i> <i>L.</i>	19-21	"
		♂	♀
"	<i>Bombus terrester</i>	8-9 mm.	9-11 "
"	" <i>hypnorum</i>	8-10 "	11-12 "
"	" <i>mastrucatus</i>	9-10 "	10-12.5 "
"	" <i>alticola</i>	9-11 "	11-13 "
"	" <i>lapidarius</i>	10-12 "	12-14 "
"	" <i>pratorum</i>	8-12 "	12-14.5 "
"	" <i>sylvarum</i>	10-12 "	12-14 "
"	" <i>proteus</i>	11-13 "	13-14 "
"	" <i>derhamellus</i> <i>K.</i>	12-13 "	13-14 "
"	" <i>agrorum</i>	12-13 "	13-15 "
"	" <i>hortorum</i>	14-16 "	19-21 "

The proboscis of the male humble-bee is 1-2 mm. shorter than that of the worker. The former therefore prefers social flowers to those of any other class, since in these the nectar is easy to get, while the female humble-bees have a preference for flowers belonging to Class **H** (Loew, 'Blumenbesuch,' I, p. 19).

The differentiation of humble-bee colonies into three different castes that develop successively (♀, ♂, ♂), limits each of them to a small set of flowers determined by the times of flowering. The males mostly appear in July, and are therefore debarred from visiting the flowers of spring and part of summer. Plants which bloom very early in the year, e.g. *Salix* and *Pulmonaria*, are visited only by queens that have survived the winter, for the first workers do not emerge till a full month after the foundations of the nest have been laid. It is only the queens, therefore, that are to be found on flowers at all times of the year. Even these become increasingly rare as autumn approaches, for the old foundress queens gradually die off, and the young queens either do not leave the nest at all or wander about idly on flowers without gathering pollen (Loew, 'Blumenbesuch,' I, p. 21).

It follows that the activity of the female bees as regards flowers differs in many ways from that of the males. This is most markedly the case in *Bombus Gerstäckeri* *Mor.* (= *B. opulentus* *Gerst.*, non *Smith*). In this species the females, as v. Dalla Torre points out (Kosmos, 1886), only visit *Aconitum Lycoctonum*, while males and workers visit as exclusively the blue species of *Aconitum*, especially *A. Napellus*.

The varying length of proboscis is the cause of this difference in habit. *B. Gerstäckeri* ♀ possesses a proboscis 18–21 mm. in length, with which it can easily suck the nectar from *A. Lycoctonum*, but the workers, having a proboscis only 11–12 mm. long, are unable to do this. 'There was, therefore, no alternative for the workers but to resort to flowers with less deeply seated nectar, and as *A. Napellus* corresponds, in regard to nectar, to *A. Lycoctonum* perhaps more than to any other plant, while at the same time both species are very conspicuous at a distance, and exhibit at the same spot racemes that rival one another in splendour, the division of spoil between queens and workers is not difficult to explain¹.'

v. Dalla Torre sees in this 'heterotrophy' an advantage to humble-bees, because it enables the comparatively short lives of these insects to be employed to the best advantage.

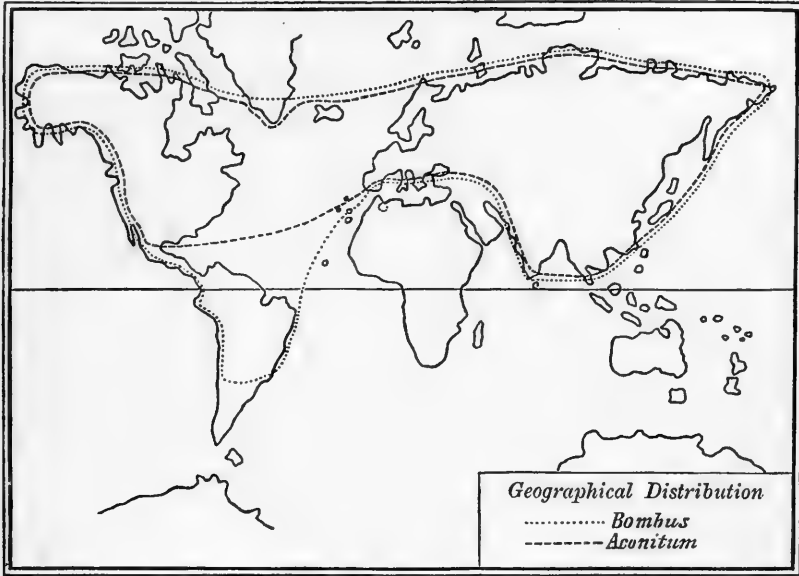


FIG. 70. Map to illustrate the distribution of *Bombus* and *Aconitum* (after Kronfeld).

With regard to the relation between the distribution of humble-bees and certain flowers that are pollinated by them, Kronfeld (*Bot. Jahr.*, Leipzig, xi, 1890, p. 19), in an interesting paper, points out that the genus *Aconitum* is dependent upon *Bombus*. He gives a map showing the areas of distribution of monkshoods and humble-bees, and a glance at this shows that the distributional area of the former is completely included in that of the latter (see Fig. 70).

The adaptations of bees to flowers are intimately connected with the length of the proboscis and the other bodily dimensions, for on the former depends, as

¹ According to Hoffer, the 'heterotrophy' of *Bombus Gerstäckeri* Mor. (in which v. Dalla Torre states that old queens exclusively visit *Aconitum Lycoctonum* L., while males and workers visit *A. Napellus* L. as exclusively) does not apply to localities where *A. Napellus* is abundant but *A. Lycoctonum* rare. In this case all three castes of the bee in question suck *A. Napellus*, as Alfken was able to prove. I have gone more fully into this in vol. II.

already shown, their fitness to suck nectar which is more or less deeply seated. The statistical investigations made by Hermann Müller, Loew, MacLeod, and myself have shown that *short-tongued bees* prefer flowers with nectar that is exposed, or not very deeply concealed, to all other kinds. They markedly affect (as do long-tongued wasps) yellow and white hues, especially social flowers and flowers with half-concealed nectar which are so coloured. To a lesser extent they seek out conspicuous social flowers, and are still less partial to flowers with completely concealed nectar, those with exposed nectar, and pollen flowers. The deeply seated nectar of bee flowers, humble-bee flowers, and lepidopterid flowers is inaccessible to them, and they therefore only occasionally appear on these as thieves (Knuth, 'Blütenbesucher,' II, p. 11). As Loew ('Einführung,' p. 378) points out, the difference in time of appearance between the two sexes has an influence on pollination in the case of the two short-tongued genera (*Andrena* and *Halictus*), which are regarded as the most important flower visitors of their kind. In *Andrena* both sexes appear at approximately the same time, while in *Halictus* only females are to be seen flying about in spring, and these are followed by parthenogenetic summer and autumn generations, the males of which are on the wing till autumn, when they perish, while the fertilized females survive the winter. The *Andrenae* seen in spring make up the chief contingent of the visitors to willow catkins, while the males of *Halictus*, which appear late in the year, visit late-flowering Composites by preference. The times of appearance of the insects and the flowering periods of the flowers, therefore, exhibit distinct mutual relations.

It has already been pointed out (p. 95) that certain species of *Andrena* visit almost or quite exclusively certain species of flowers, and that the species of *Prosopis* seek out by preference flowers with a strong odour.

The short-tongued bees of the Alps (H. Müller, 'Alpenblumen,' p. 520) are very distinctly superior to wasps as regards adaptation to flowers. In species where the nectar is externally visible (**E** and **EC**), wasps make up more than half of the visitors, not a quarter of them being bees. The latter most decidedly prefer flowers with completely concealed nectar, although their visits are divided among flowers in all stages of specialization.

The visits of *long-tongued bees*, in accordance with their structure, are chiefly paid to bee and humble-bee flowers, and also to brightly coloured Composites; in less degree to lepidopterid flowers, and to white or yellow social flowers with concealed nectar; and still less to flowers with half-concealed nectar and to pollen-flowers. Flowers with exposed nectar are visited by them very rarely indeed (Knuth, 'Blütenbesucher,' II, p. 11). They show a strongly marked preference for red, blue, and violet colours.

Solitary long-tongued bees were never met with in the Alps (H. Müller, 'Alpenblumen,' p. 521) on flowers with freely exposed nectar, and only one-tenth of their visits were paid to flowers with nectar that was clearly visible though not quite fully exposed. On the other hand, 85 % of their visits were to flowers with completely concealed nectar, and almost half of these were typical bee flowers.

Social long-tongued bees are influenced ('Alpenblumen') by the necessity for rifling as completely as possible the maximum number of flowers, for with increase in the number of individuals the demand for food increases. Even flowers with

completely exposed nectar that have been passed over by the solitary long-tongued bees are not despised by the social forms.

The honey-bee occupies a special place among the species that are most specialized with reference to flowers. As I was able to show in my work, 'Blumen und Insekten auf den nordfriesischen Inseln' (pp. 174, 175), *Apis*—at least in the district referred to—visits flowers of all classes and colours, though certainly giving preference to bee flowers. My later statistical investigations showed that the honey-bee also visits with special zest conspicuous social flowers, and flowers with nectar completely or partly concealed ('Blütenbesucher,' II, p. 10).

Hermann Müller obtained precisely similar results. In a hundred visits paid by the honey-bee, he observed that the various classes of flowers received the following numbers:—

	<i>In the Lowlands. In the Alps.</i>	
An and Po	7.2 . . .	8.9
E	8.7 . . .	3.6
EC	13.6 . . .	7.1
C	20.8 . . .	19.6
S	13.3 . . .	23.2
H	35.2 . . .	37.5
L	1.1 . . .	0.0

It appears from these results that *Apis* prefers bee flowers, but also readily visits social flowers and flowers with concealed nectar, as well as, in the lowlands, flowers with half-concealed nectar. It follows, therefore, that the honey-bee occupies an intermediate position between long-tongued and short-tongued bees as regards its choice of flowers. The same thing is true of its colour predilections.

Loew ('Blumenbesuch von Insekten,' I, pp. 6 et seq.) asserts that there is a double reason why the honey-bee takes the foremost place among insects which visit flowers, besides intelligence, in which it surpasses all its competitors. For the work of pollination the constantly increasing community of the beehive surpasses humble-bee societies and solitary bees, because it is able from the beginning of spring till late autumn to send forth at any time a great number of individuals well adapted to the requirements of flowers. No other bee can do this with the same continuity. There are, in addition, physical advantages apart from the special structure of the collecting and suctorial apparatus, by far the most important of these being the *medium* length (6 mm.) of the proboscis. It is true that greater elongation of this organ would render a number of humble-bee flowers accessible to the honey-bee, from which it can now only obtain nectar by biting a hole, but the possession of a longer proboscis would oblige it to give up visiting many flowers with nectar entirely or almost entirely exposed, for these cannot be conveniently rifled by long-tongued visitors. Considering the honey-bee's particularly large requirements in the matter of larval food, a proboscis of medium length would appear to be the best conceivable equipment for enabling it to take precedence of all competitors in regard to the number of flowers despoiled.

Humble-bees also visit flowers of all classes, but greatly prefer humble-bee flowers, bee flowers, lepidopterid flowers, and conspicuous social flowers; to a

lesser degree they show preference for flowers with concealed nectar (Knuth, 'Blütenbesucher,' II, p. 10).

Humble-bees differ as regards the flowers they visit according to the length of their proboscis. The longer this is, the more exclusively do they seek out flowers belonging to Class **H**; the shorter it is so much the more do they also visit flowers with less deeply concealed nectar, and show an increasing disposition to steal nectar by biting holes. *Bombus hortorum*, which has a longer proboscis than any other of our native humble-bees, shows a more decided preference for the flowers of Class **H** than any of its allies, and has never been observed stealing nectar, while *B. terrester*, our shortest-tongued species, is especially fond of biting through corolla-tubes, in order to steal nectar through the openings thus made. The hive-bee often steals nectar through holes bitten by this and other species of humble-bee.

A. Schulz ('Beiträge,' II, pp. 203-24) names 165 species of plants with flowers thus bitten through which he has observed in the lowlands and in the Alps. The following table summarizes his observations on bees which treat flowers in this way:—

Name of Bee.	Length of Proboscis in		Percentage of perforations made.	Number of species with perforated flowers.
	♀	♂		
	mm.	mm.		
<i>Bombus mastrucatus</i> Gerst.	10-13	9-11	50	51
<i>B. terrester</i> L.	9-11.5	8-9.75	35	125
<i>B. lapidarius</i> L.	12-14	9.5-12	15	40
<i>B. pratorum</i> L.	12-14.5	8.5-12		24
<i>B. Rajellus</i> K. (<i>B. derhamellus</i>) .	13-14	11-13		19
<i>Apis mellifica</i> L.	—	5.5-6.5		11
<i>Bombus alticola</i> Kriechb.	10-13	9-11.5		11
<i>B. soroënsis</i> Fabr. var. <i>Proteus</i>				
<i>Gerst.</i> (and others)	13-14	10-13		9
<i>B. lapponicus</i> Fabr.	12-13	9-12		7
<i>B. mesomelas</i> Gerst.	15-18	12-14		1

Except, therefore, in *Bombus mastrucatus*, we see that the tendency to perforate flowers diminishes as the length of proboscis increases, the explanation being that elongation increases the possibility of obtaining nectar in a normal manner from deeper flowers. Among seventy-six visits of *Bombus mastrucatus* to various flowers, observed by Hermann Müller in the Alps, there were thirty-four cases of nectar theft. This humble-bee—called by Müller (*Kosmos*, v, p. 422) 'an anti-teleologist among the visitors of alpine flowers'—is distinguished ('Alpenblumen,' p. 586) above all others, even *B. terrester*, by its very decided habit—an unfortunate one for flowers—of biting holes in order to get at the nectar of deeply placed nectaries to which access is difficult.

F. Ludwig, in his review (*Bot. Centralbl.*, Cassel, xxxvii, 1889, pp. 355-7) of a memoir by L. H. Pammel ('On the Pollination of *Phlomis tuberosa* L. and the Perforation of Flowers,' *Trans. Acad. Sci.*, St. Louis, Mo., v, 1888, pp. 241-77), states

that this author, in summarizing previous observations, mentions 133 plants in which perforation has been noticed. A. Schulz rightly remarks ('Beiträge,' II, p. 203, note 3) that if the review is a full one this memoir cannot claim to be absolutely exhaustive.

Hermann Müller speaks as follows ('Alpenblumen,' pp. 521, 522) with regard to the visits of *parasitic humble-bees* to flowers. From a high degree of adaptation to flowers, which was necessary when they reared their own offspring, they have lapsed into brood-parasitism, retaining only such adaptations as are requisite for their own maintenance. In consequence they have certainly not become more specialized in relation to flowers than their social ancestors, which collected the food necessary for their communities. They possess, at most, some amount of inherited skill which is displayed during their visits to flowers, though it is no longer exercised for the benefit of a community. What then do we find here? Anemophilous flowers, pollen flowers, and flowers with nectar completely exposed, or only partially concealed yield far too little food to be ever touched by these parasitic humble-bees, which only have to provide for themselves, and are, therefore, perfectly free to follow their own inclinations and consult their own convenience. They never attempt to plunder lepidopterid flowers, for such endeavours are exhausting and often fruitless even for humble-bees. The rich supplies of nectar readily accessible to them in nectar flowers and social flowers with completely concealed nectar (CS) constitute the only and never-failing goal of their activity, and their proceedings are of an easy-going character that is quite unparalleled among humble-bees collecting food for the benefit of a community. When we consider that even bee flowers are visited by them but rarely, and that most of their visits are paid to Composites and allied plants, which are easy to plunder and offer a rich booty, we can scarcely avoid the conclusion that, since relinquishing the task of rearing their own brood, they have become less skilled in plundering specialized bee flowers, or even if they fully retain this aptitude the easy parasitic life prevents its full exercise.

The eloquent account given by Hermann Müller led me ('Blütenbesucher,' I, p. 6; II, p. 10) to test the correctness of his views, and I reached the following conclusion.—Parasitic humble-bees chiefly visit brightly coloured social flowers, and next to these prefer flowers with concealed nectar, bee flowers, white and yellow social flowers, and humble-bee flowers, while now and then they even visit flowers with half-concealed nectar, but they avoid anemophilous flowers, pollen flowers, flowers with exposed nectar, and lepidopterid flowers.

The habit possessed by female humble-bees of chiefly seeking out hymenopterid flowers, while the males give preference to social flowers, is exaggerated in the parasitic genus *Psithyrus*, which constitutes a small side-branch of the group. The species of this genus consequently prefer dark-coloured flowers even more than do the short-tongued species of *Bombus* (Loew, 'Blumenbesuch,' I, p. 35).

The suctorial apparatus of *Anthophora*, *Eucera*, *Melecta*, *Megachile*, *Osmia*, *Anthidium*, *Heriades*, *Chelostoma*, *Stelis*, *Coelioxys*, and the remaining long-tongued *Apidae* in general, corresponds with that of *Apis*, *Bombus*, and *Psithyrus*, especially in the often marked elongation of the ligula and its sheath.

The species of *Anthophora*, like humble-bees, greatly prefer the flowers of

Class **H**, and also show the same liking for dark-coloured blossoms. *Anthophora pilipes* *F.* (= *A. acervorum* *L.*), which has a proboscis 19–21 mm. long, visits almost exclusively the flowers of Class **Hh**, with nectar concealed as deeply as possible, and agrees precisely in this respect with *Bombus hortorum* *L.*, which has a proboscis of the same length. Owing to its earlier appearance, however, it is only found on spring-flowers, such as *Corydalis cava*, *Pulmonaria officinalis*, *Lamium purpureum*, and species of *Primula*. Later on in the year its visits to the longest-tubed humble-bee flowers are replaced by those of *Bombus hortorum*.

Eucera longicornis *L.*, in accordance with the length of its proboscis (10–12 mm.) visits bee flowers by preference, especially papilionaceous ones. This bee also shows a special liking for dark-coloured flowers, and the same is true for species of *Megachile*, *Osmia*, and most other long-tongued Apidae (except *Heriades truncorum* *L.*). Loew ('*Blumenbesuch*,' I, p. 54) shows that this colour-preference is not dependent upon the length of the proboscis, but is a specific peculiarity.

The long-tongued bees exhibit very great constancy in their choice of flowers. I saw ('*Blütenbesucher*,' I, p. 4), for example, the honey-bee, for the space of several minutes sink its proboscis almost every second into one flower after another of *Trifolium repens*, without seeking out any other species. Sometimes it spent a few seconds sucking from one flower, but on an average it made thirty to forty visits in a minute.

I noticed exactly the same thing when I observed the visits made to flowers by another long-tongued bee. On the 2nd of May, 1897, I had the opportunity of counting, watch in hand, such visits in the case of *Anthophora pilipes* *F.* ♀ (= *Podalirius acervorum* *L.*). The bee visited *Lamium purpureum*, and had already collected considerable masses of orange-yellow pollen: it now flew from flower to flower of the species named, doing nothing but suck nectar. Only once, in passing, it sucked from *Viola tricolor* var. *arvensis*. In two and a half minutes it made seventy-two visits, so that on an average a visit lasted about two seconds. The duration of the act of sucking was as long as five seconds in some flowers which apparently afforded a richer booty than most others. As a rule, however, the bee stayed for a second, sinking the proboscis rapidly into the base of the flower, withdrawing it as rapidly, and then buzzing away to another blossom. During the acts of sucking the humming noise emitted during flight was of course interrupted, so that the number of separate visits could be determined from these interruptions. As I had heard the *Anthophora* from one to two minutes¹ before I saw it, and during this time the humming was interrupted every second or two, it follows that the bee exerted its activity among the flowers for at least four minutes, and in this time pollinated far more than 100 flowers.

E. Loew ('*Blumenbesuch*,' I, p. 93) has proved for almost all genera of bees, that besides length of proboscis, some other adaptational factor helps to determine the selection of flowers, and may have such an influence that, e.g., a long-tongued

¹ I did not measure this period with the help of my watch, but by counting the number of my respirations. As I breathed nineteen times a minute, this gave about three seconds for each respiration, and afforded me an excellent way of estimating small periods of time with great accuracy.

species of bee may visit flowers with exposed or partly concealed nectar more readily than bee flowers (*Osmia rufa* L. ♂), while another may prefer bright instead of dark colours (*Heriades truncorum* L.). Neither the two sexes of the same species nor the various species of the same genus, nor genera of the same family with proboscis of equal length, are restricted in their visits to flowers, as might be theoretically expected by the purely mechanical determinant afforded by the length of the proboscis. Nest-building, early or late time of appearance, special preference of the larvae or adults for pollen as food, and so forth; all these factors influence the selection of flowers, at least as much as this depends upon the structure and length of the proboscis in the insect pollinator. The principle emphasized by Hermann Müller of arranging bees in an ascending series according to the length of the proboscis, from those in which this organ is very short to those in which it is very long, is consequently one-sided, and Loew has therefore undertaken a more comprehensive classification (cf. pp. 192-5).

THE OTHER HYMENOPTERA

play a much less important part as agents of cross-pollination than bees, which have now been dealt with. The latter (except short-tongued species) are the most highly organized visitors to flowers, and there are a large number of mutual adaptations between their structure and that of flowers. Loew therefore terms the highly specialized Apidae *eutropous* (i.e. well-adapted) insects, while he describes those which are in a lower stage of specialization as *hemitropous* (i.e. half-adapted). (Cf. pp. 193-4.) Following Hermann Müller (p. 149) it has already been emphasized that the least specialized bees hardly stand on a higher morphological level as regards adaptation to pollination than the *fossorial wasps* (Sphegidae). The latter, however, are less concerned with flowers in that only the adults use these as a source of food, for they do not provide their larvae with pollen and honey, but with spiders, insects, or insect larvae, which have been paralysed or killed by stinging. The structure of their mouth-parts, as already stated, agrees on the whole with that of *Prosopis* and *Sphecodes*, but the mentum and maxilla are still shorter and less narrow. A pollen-collecting apparatus does not occur, as is but natural considering the way in which their young are fed.

In their mode of visiting flowers, the Sphegidae never display the certainty, one might almost say geniality, with which most bees are able to recognize the objects of their predilection from considerable distances. This perhaps depends upon a lower development of their olfactory organs. The visits of fossorial wasps are more especially paid to the flowers of classes **E**, **EC**, **C**, **S**, and **Hw**. (Loew, 'Blumenbesuch,' II, p. 98.)

True wasps (Vespidae), considered as visitors to flowers, may be divided (Loew, op. cit., II, p. 100) into two groups. The members of the first (including the social genera *Vespa* and *Polistes*) nourish themselves only occasionally upon flower-food, but also feed on the juices of plant-lice, sweet fruits and other edibles, raw beef, sugar, and the soft parts of captured insects (flies, bees, Lepidoptera). The members of the second group (including the solitary genera *Eumenes*, *Discoelius*, *Odynerus*, and *Pterocheilus*), when adult, live upon flower-food only. There is a corresponding difference in the formation of the ligula. It is only in the second

group that this organ and the labial palps are obviously long and narrow, while in the genus *Pterocheilus* a peculiar feathering of the latter is also seen. Only this group can therefore be placed on the adaptational level of the fossorial wasps—the stage described by Loew as *hemitropy*—while the social wasps, owing more particularly to their omnivorous habits, do not display any obvious adaptations enabling them to pilfer flowers successfully—a condition which Loew terms *allotropy* (cf. p. 193). On the other hand, certain flowers are visited by wasps with marked predilection, so that Hermann Müller was able to establish a special group of ‘wasp flowers’ (see pp. 119–20), the visitors of which, however, belong to many other groups of insects besides ‘wasps.’

The visits of true wasps to flowers, like those of fossorial wasps, are made in order of decreasing preference to flowers with exposed or partly concealed nectar, flowers with completely concealed nectar, social flowers and wasp flowers, while bee flowers and pollen flowers are most avoided.

The *ichneumons* (Ichneumonidae) are only casual flower visitors, but at the same time they display a certain preference for particular species, so that these may be described as *ichneumon flowers* (cf. p. 121). *Saw-flies* (Tenthredinidae), like ichneumons, are only occasional allotropous flower visitors. Details have already been given (pp. 103–5) with regard to the peculiar part played by certain fig-insects (*Blastophaga*, *Sycophaga*) in the pollination of figs.

Among the *Ruby wasps* (Chrysididae) the genus *Parnopes* has a longish proboscis adapted for visits to flowers, while species of the other genera, though not infrequently met with on flowers, are of no importance as agents of pollination. The *Wood wasps* (Siricidae) which belong to this group have not yet been observed visiting flowers.

Ants (Formicidae), lastly, frequently occur as ravagers of flowers, for which reason Loew has termed them *dystropous*.

Forms other than bees among Hymenoptera, which Hermann Müller places together (‘*Alpenblumen*,’ p. 518) under the name of ‘wasps,’ mainly visit in the Alps flowers with directly visible nectar, where they chiefly come into competition with beetles and short-tongued flies. On pollen flowers only saw-flies and true wasps were met with, but these appeared to be attracted by the chance of capturing flies rather than by the pollen. On alpine lepidopterid flowers saw-flies occur, as well as true wasps, and also occasional ichneumons, though these benefit neither themselves nor the flowers. Ants insinuate themselves into flowers not infrequently, and sometimes reach the nectar. But they are, as a rule, quite useless as agents of pollination, not only for these flowers, but also for others they visit. This is partly because they are too small for this office, and partly because they go on foot, and stay for a long time at any supply of nectar they may have found. Ichneumons and solitary true wasps use the holes bitten by *Bombus mastrucatus* in bee flowers, and share the stolen nectar, so that they too may be regarded as mere enemies to bee flowers. Social wasps (*Polistes*, *Vespa*), on the other hand, are not found on the most highly specialized bee flowers, but considered as agents of pollination are practically divided between such of these as are of lower grade (*Rubus Idaeus* and *R. Saxatilis*, **CH**) and wasp-flowers (*Cotoneaster vulgaris*, *Lonicera alpigena*, **Hw**).

Only a minority of the diverse visits of the wasps here mentioned are devoted to plundering flowers and social flowers with fully concealed nectar (**C, S**), while sawflies only visit flowers from which they can get nectar by simply bending down their heads.

As regards the colours they have acquired by natural selection, wasps on the whole are also to be looked upon as but little specialized flower visitors. More than three-quarters of the species of all their families, and in ichneumons (which as a rule only seek for entirely exposed nectar) even nine-tenths, are greenish, white, or yellow. (H. Müller, 'Alpenblumen,' pp. 519-20.)

B. Butterflies and Moths (Lepidoptera).

Hymenoptera are undoubtedly the most important of all our indigenous insects as regards pollination of flowers, and for that reason have been first described. But in respect of adaptation to flowers, they are surpassed by the Lepidoptera, since all these seek for nectar as their only food, whereas many Hymenoptera nourish

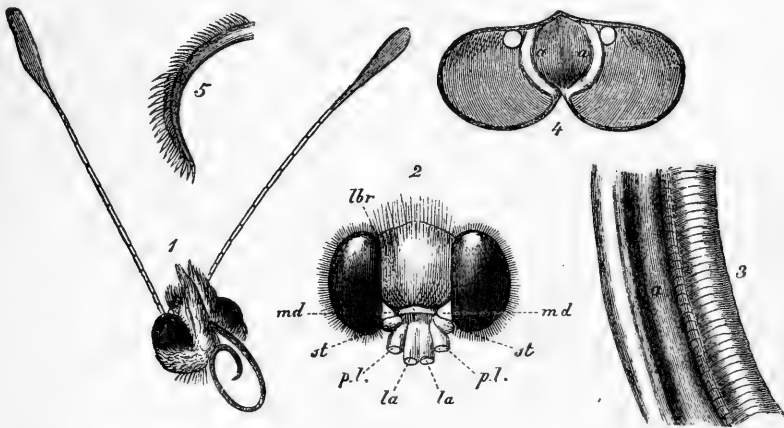


FIG. 71. *Adaptation of Lepidoptera to flowers* (after Hermann Müller). (1) Head of *Polyommatus phloea* L., with proboscis half rolled up. (2) Head of *Vanessa Io* L.; the laciniae and the labial palps have been cut off short ($\times 7$). (3) Part of a lacinia of *Macroglossa fuciformis* L., seen from the inner side (*a*, the groove); highly magnified. (4) Transverse section through the apposed laciniae of the same species highly magnified. *aa*, tube formed by the juxtaposition of the two grooves. (5) Tip of a lacinia of *Vanessa Atalanta* L. References in (2) as in Fig. 64.

themselves upon animal substances as well as flower-food, and not a few of them even prefer such a diet.

As the Lepidoptera are exempt from the care of offspring, simply laying their eggs on the food-plant of the caterpillar, their proboscis is exclusively adapted for securing the nectar that serves as their only nourishment. In the mouth-parts of this order (Fig. 71), the labrum (2, *lbr*) and mandibles (*md*) are rudimentary, but the labial palps and first maxillae are well developed. The laciniae of the latter are produced to form two long half-tubes, which lie so close together that they constitute a closed suctorial tube. According to Kirbach, the adjacent edges of the maxillae are provided above and below with sickle-shaped plates lying close together, or are beset on the lower side with a row of double hooks, which interlock and bind these

structures very closely together. These arrangements keep the two maxillae in as close contact as possible, at the same time making the canal practically air-tight, without, however, interfering with the flexibility of the whole organ.

The proboscis of the Lepidoptera, which is sometimes very long, is rolled up under the thorax when not in use. To render this possible the outer chitinous walls of the laciniae are transversely striated.

By means of this simple arrangement, says Hermann Müller ('Fertilisation,' p. 5), Lepidoptera are able to penetrate flowers of the most varied forms, both flat and long-tubed, and to feed on their nectar. Peculiar stiff, pointed appendages at the ends of the laciniae (Fig. 71, 3) also enable them to tear open delicate succulent tissues, and they are therefore able to utilize the sap of such flowers as do not secrete free nectar. That they actually make use of this apparatus has been proved by direct observation, for Lepidoptera are now and then to be found sucking flowers which secrete no free nectar, e.g. *Cytisus Laburnum*, *Erythraea Centaurium*, and the like. At the Cape, Lepidoptera damage peaches and plums by boring through the epidermis with their proboscis at spots that are quite intact (Ann. Mag. Nat. Hist., London, xxiv, 1869).

The length of the proboscis of Lepidoptera varies greatly, as the following table shows:—

	<i>mm.</i>
Bombycidae	1-4 (exceptionally up to 10)
Pyalidae	4-9
Geometridae	4-12
Zygaenidae	7-11
Noctuidae	7-19
<i>Plusia gamma</i>	15-16
Rhopalocera	5-28
<i>Lycaena semiargus</i>	7-8
<i>Argynnis Pales</i>	9-10
<i>Vanessa Atalanta</i>	13-14
„ <i>cardui</i>	13-15
„ <i>urticae</i>	14-15
„ <i>Io</i>	17
<i>Papilio Machaon</i>	18-20
<i>Parnassias Apollo</i>	12-13
<i>Anthocharis cardamines</i>	12
<i>Pieris brassicae</i>	16
„ <i>napi</i>	10-12
„ <i>rapae</i>	13-18
<i>Rhodocera rhamni</i>	16-17
<i>Coenonympha Pamphilus</i>	7
<i>Epinephele Janira</i>	10
Sphingidae	3-80
<i>Smerinthus tiliae</i>	3
<i>Macroglossa stellatarum</i>	25-28
<i>Sphinx ligustri</i>	37-42
„ <i>convolvuli</i>	65-80

Some of the extra-European Sphingidae, especially tropical species, have a proboscis 140–160, or even up to 250 mm. long. There are corresponding flowers with corolla-tubes or spurs 6–12 cm. in length (*Oenothera Missouriensis*, *Habenaria*, *Gardenia*, *Randia*, *Portlandia*, *Exostemma*, *Oxyanthus*, *Angraecum sesquipedale*). Fritz Müller found the proboscis of *Macrosilia Cluentius* Cr. to be about $\frac{1}{2}$ m. long.

The choice of flowers by Lepidoptera is generally correlated with the length of the proboscis, forms in which it is long preferring flowers with deeply seated nectar. Corresponding to hawk-moths (Sphingidae) which have a greatly elongated proboscis, there are special forms of flowers that are mainly or entirely adapted to their visits, and for this reason Loew describes these moths as *eutropous* insects in contrast to the other *hemitropous* Lepidoptera ('*Blumenbesuch*,' II, p. 127). The majority of the hawk-moths fly about on mild summer evenings at dusk or night. And as such evenings are not very common in our climate, the period of flight of these and other moths is very restricted. Hermann Müller supposes ('*Fertilisation*,' p. 67) that either the shortness of the time when the weather is suitable for their flight, or the pursuit of bats, may be the cause of the extraordinarily rapid and stormy movements of these moths. This peculiarity of crepuscular and nocturnal Lepidoptera is a decided advantage to the flowers they visit, for the amount of pollination effected by every visitor in a given period of time is in proportion to the shortness of its stay at each flower and the rapidity of its flight to the next. Hawk-moths demonstrate, in a most marked manner, the advantage of rapid pollination for plants. Hovering before the flower, they introduce their long proboscis into the corolla-tube, and after a short delay hasten with stormy flight to another flower. Among nocturnal flowers, therefore, most are adapted to these very Lepidoptera, having the nectar concealed at the bottom of such long tubes or spurs that it is accessible to them alone ('*Fertilisation*,' p. 67).

While most hawk-moths visit flowers at dusk, the species of the genus *Macroglossa* also fly about in the daytime¹, and do so in the same stormy manner as their nocturnal relatives. A distinction can therefore be made between *night hawk-moth* and *day hawk-moth* flowers.

I have described in the case of *Macroglossa stellatarum* ('*Bl. und Ins. auf. den nordfries. Ins.*,' p. 80) the way in which hawk-moths visit a flower.—The insect comes with impetuous flight in the bright sunshine of high noon to the flowers of *Lonicera Periclymenum*, halts and hovers with trembling wings in front of the entrance to the flower, and sinks the extended (22–28 mm. long) proboscis deep into the corolla-tube, thus effecting cross-pollination. The proboscis is withdrawn as quickly as it was introduced, and the insect forthwith flies straight as an arrow to another flower, there to repeat the same actions. The species of *Sphinx*, and other genera, when visiting a flower at dusk or night behave precisely in the same way as this diurnal hawk-moth.

With what skill and persistence the Sphingidae suck deeply hidden nectar from their flowers, and with what fidelity they adhere to the species once selected, thus

¹ Many Noctuidae also sometimes fly by day, e.g. *Plusia gamma*. Hermann Müller ('*Alpenblumen*,' pp. 64 and 66) observed in the Alps several crepuscular and nocturnal moths flying by day to *Gymnadenia conopsea* and *G. odoratissima*.

unconsciously effecting its pollination, appears from the following observations of Hermann Müller ('Alpenblumen,' pp. 156, 339, 341, 362).—At the summit of the Albula Pass this observer saw a *Macroglossa stellatarum* visit several hundred flowers of *Primula integrifolia* in the space of a few minutes. Another individual, in the same short time, visited several hundred flowers of *Gentiana verna*, *G. bavarica*, and *Viola calcarata*, as well as several blossoms of *Gentiana excisa*. Two more of these moths visited, respectively, 106 flowers of *Viola calcarata* in barely four minutes, and 194 in $6\frac{3}{4}$ minutes.

Diurnal Lepidoptera act quite differently when visiting flowers. Hermann Müller (*Kosmos*, iii, p. 424) gives an exceedingly accurate and attractive picture of the way in which butterflies behave.—They pay their visits to flowers in an easy, playful way, not like earnest workers for a living, but as if it were, next to love-making, the most agreeable amusement in the warm sunshine. Flowers are their public pleasure resorts, which offer them in addition to the sweet pleasures of nectar, the most favourable opportunity of exhibiting their gay clothing, and entering upon affairs of love. But they are ready at any moment to forsake the blossoms, be it to whirl through the air with the first good comrade that by chance appears, or to flutter after a female, or to flee from an imaginary danger.

According to Delpino ('Ult. oss.,' *Atti Soc. ital. sc. nat.*, Milano, xvi, p. 345), male butterflies (*Pieris*, *Rhodocera*, *Limenitis*, and others) pursue the females unceasingly, so that they pass with great rapidity from the inflorescence of one plant to that of another. This habit increases in very high degree the probability of the cross-pollination of different stocks.

Lepidoptera, especially the moths, possess an exceedingly keen sense of smell. Delpino (op. cit.) relates that having left a female of *Bombyx Pavonia major* in a small case at a half-open window, three males had joined the female on the following morning, having apparently been attracted by her odour, although this could not be perceived by Delpino himself. Attention has already been called (p. 125) to Kerner's experiment with *Sphinx convolvuli*, which proves the keen sense of smell of this moth.

Lepidoptera are hence very aptly termed the 'flowers of the air'—an expression first used by Jean Paul (cf. *Kosmos*, i, p. 260)—not only on account of their brilliant colour, but also in some cases because of their odour. According to Fritz Müller (*Kosmos*, iii, p. 187), the odour of the hind-wings of *Papilio Grayi* (a native of South Brazil) is so strong and aromatic that this investigator carried the insect about in his hand for the purpose of smelling it from time to time like a flower. The male of another butterfly, *Morpho Adonis*, smells like vanilla (Fritz Müller, op. cit., p. 419), as do many lepidopterid flowers.

The *odoriferous organs* which occur in many Lepidoptera (and rarely in other insects) are only found in the males, the odours proceeding from which undoubtedly attract and stimulate the females. These odours are exhaled from modified scales known as *androconia*, which vary greatly in form, arrangement, and position. They are generally situated on the wings, more rarely on the trunk or tibiae. Ethereal oil passes up from cells lying at the bases of these scales, is distributed over them, and then evaporates. The resultant odour can be clearly perceived on the fingers, after wiping the dust from the wings of a living male *Pieris napi* or *rapae*. The

androconia in these cases, as in many other butterflies, are situated on the front margin of the hind-wings, where there are spots resembling fungi ('brands'), which consist of brush-shaped erectile structures. To avoid unnecessary evaporation, these organs are covered by the hinder margins of the front wings, and for the same reason the androconia are usually found on the upper surface of the wings of butterflies, which rest with their wings folded together vertically. Some Lepidoptera possess odoriferous organs on the trunk, e.g. in some male hawk-moths they occur on the under-side of the base of the abdomen. In *Sphinx ligustri*, *S. pinastri*, and *Acherontia atropos* the androconia are well developed, in *Deilephila euphorbiae* they are considerably less so. Similar organs also occur on the abdomen of some owlet-moths. More rarely they are situated on the thorax (in the hawk-moth genus *Chaerocampa*), and somewhat more frequently on the legs (many Noctuidae and Geometridae, some Hesperiidae, and others).

According to my statistical investigations ('Blütenbesucher,' II, p. 11), hawk-moths confine their visits almost entirely to lepidopterid flowers, the long corollatubes or spurs of which correspond to their long proboscis. Occasional visits are also paid to flowers of Class H, from which the insects know how to skilfully steal the nectar.

Social flowers which can be seen a long way off exercise the greatest attraction on the remaining Lepidoptera, also the lepidopterid flowers which suit their long proboscis, flowers with concealed nectar as deeply situated, and bee flowers. In the Alps, which are particularly rich in Lepidoptera, these insects are compelled to visit even such flowers as possess less conveniently situated nectar. In their necessity they there make trial of even pollen flowers, which offer them nothing, or from which by boring they are perhaps able to obtain a trace of sap.

Members of the most diverse groups of the excessively abundant alpine Lepidoptera (H. Müller, 'Alpenblumen,' p. 524) visit flowers in all stages of adaptation, but they prefer secreted nectar to that which is enclosed in the tissues, concealed nectar to that which is exposed, and social flowers to those which have to be plundered one by one. They display such a preference for the social flowers of Composites and related forms, that these receive from a third to about a half of all their visits, which is almost without exception a far greater number than the lepidopterid flowers and bee flowers together receive.

With increasing length of proboscis (op. cit., p. 525) the Lepidoptera turn more and more away from the shallower to the deeper supplies of nectar. For the silver-Y moth (with a proboscis 15-16 mm. long) social flowers (S) cease to be the favourites, the majority of its visits being made to the more abundant stores of bee flowers and lepidopterid flowers. In the Alps as much as 94 % of the visits of *Macroglossa stellatarum* (with a proboscis 25-28 mm. long) are paid to such forms, exactly half these visits being to bee and humble-bee flowers, and half to lepidopterid flowers.

With regard to colour preference, it has been shown both by the observations of Hermann Müller and by the investigations of E. Loew ('Blumenbesuch,' II, p. 129) that Lepidoptera markedly prefer dark colours to bright ones. Reference has already been made (pp. 124, 144) to the preference of certain Lepidoptera for flowers resembling their own wings in colour.

C. Flies or Two-winged Insects (Diptera).

In Hermann Müller's opinion ('Fertilisation,' p. 36) most species of flies probably visit flowers, but this only applies to the first main division of the order, the *Diptera brachycera*, which are of very great importance in relation to pollination, while the species of the second great division, the *Diptera nematocera*, are almost useless in this respect, only some of the Tipulidae being common visitors of flowers, while a few tiny moth-flies (Psychodidae) pollinate Aristolochia, Arum, Adoxa, and Chrysosplenium. It will therefore suffice to describe the organs employed in procuring nourishment from flowers, and the way they are used in those flies which are of special importance for the transference of pollen. I think that this cannot be done better than by following the admirable account given by Hermann Müller ('Fertilisation,' pp. 36 et seq.).

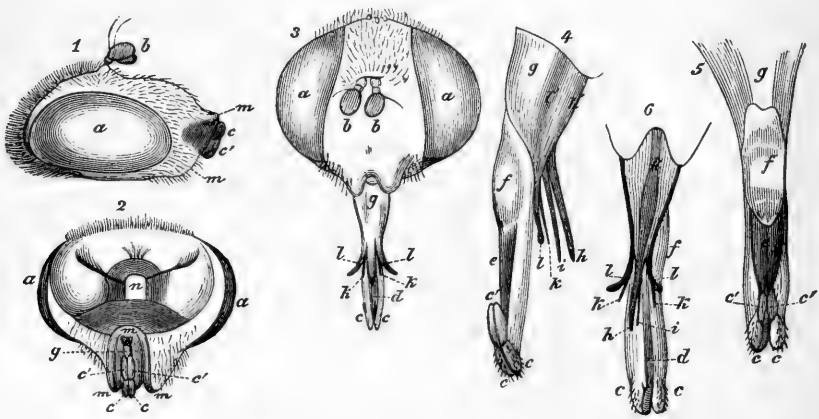


FIG. 72. Mouth-parts of *Eristalis* ($\times 7$) (after Hermann Müller). (1) Head of *E. arbustorum*, with retracted proboscis; from the side. (2) Ditto, from below. (3) Ditto, with extended proboscis; from above. (4) Extended proboscis of *E. tenax*; from the side. (5) Ditto, from below. (6) Ditto, from above. *a*, eye; *bb*, antennae; *cc*, end-flaps of proboscis; *c'c'*, their inferior segments; *d*, groove on the upper side of the tip of the proboscis; *f*, contractile middle part of the proboscis; *g*, contractile base of proboscis; *h*, upper lip (labrum), grooved below to receive the unpaired piece (*i*), which probably represents the two fused mandibles; *k*, maxilla; *l*, maxillary palp; *m m*, edges of the cavity on the under-side of the head into which the entire proboscis is withdrawn; *n*, occipital foramen.

The family of *Hover-flies* (Syrphidae) includes those well-known insects which hover as if fixed to a point in the air, then rapidly dart to one side and act as before. They contribute far more to the pollination of our native flowers than all the other Diptera put together, for most of their numerous and often very common species mainly or exclusively depend on flower-food, and in connection with this they exhibit very special adaptations for securing pollen and nectar alternately. To illustrate the mouth-parts of flies, and their relation to flowers, H. Müller therefore selected *Eristalis* and *Rhingia*, two hover-flies which are highly developed in this respect, and at the same time very common.

In *Eristalis* the completely extended proboscis is clearly seen to be composed of three successive segments (Fig. 72, 4, 5, 6, and Fig. 73, 1).—(1) The membranous basal piece (*g*), which bears at its front end two unpaired (*h*, *i*) and two paired (*k*, *k*)

elongated chitinous pieces, with two palps (*l*, *l*) external to the latter. (2) The equally membranous and very contractile middle segment (*f*), which, however, is clearly demarcated on the lower side only. (3) The tip of the proboscis, which is supported beneath by a stiff chitinous plate (*c*), and bears at its apex two contiguous bifid flaps or lips (*c c* and *c' c'*), while its upper surface is traversed by a longitudinal groove (*d*). Of the chitinous pieces at the end of the basal segment of the proboscis, the upper unpaired one (*h*), which is prolonged under the skin to the head (Fig. 72, 4, 6, *h*), can be regarded as an upper lip (labrum): while the lower

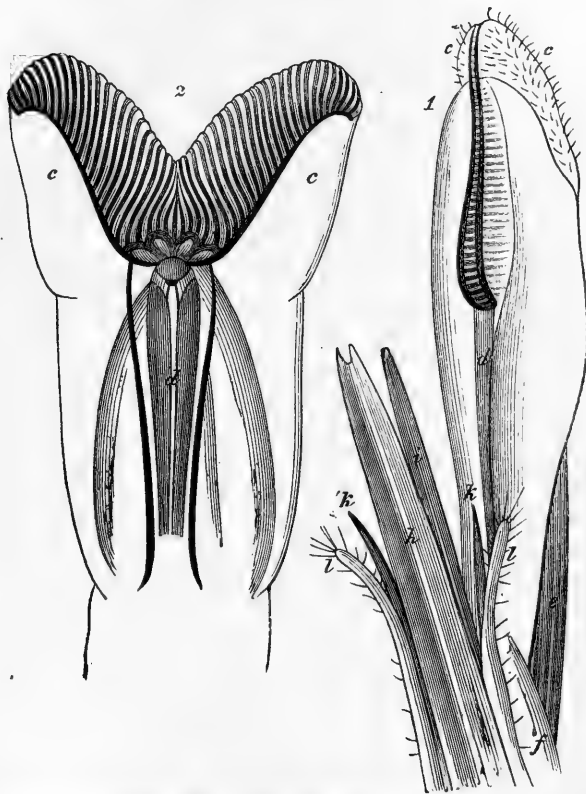


FIG. 73. *Proboscis of Eristalis tenax, highly magnified* (after Hermann Müller). (1) Most of the proboscis of *Eristalis tenax* L., with the flaps applied together and the mouth-parts slightly separated; seen from the right and above. When the pieces *h* and *i* are pressed down into the groove *d*, the mouth-parts are in the position for feeding on pollen. (2) The end of the same proboscis with the end-flaps pressed apart to show the chitinous ridges on their inner sides. References as in Fig. 72.

unpaired one (*i*) seems to have been formed by fusion of the two mandibles. The concave side of the upper lip (*h*) serves as a downwardly directed groove, into which the piece *i* can be completely withdrawn. The small mouth-opening can be seen between the bases of these pieces *h* and *i*, when they are drawn widely apart. The free ends of the two sharp chitinous pieces (*h h*) arise on either side somewhat below the fused mandibles (*i*), and bear palps on their outer sides. These are therefore undoubtedly to be looked upon as the laciniae with their maxillary palps, while the bases of the maxillae have fused with the bases of the lower lip (*g*) (labium), and are

dimly visible through the skin (Fig. 72, 4 *l'*). The contractile piece (*f*) and the piece supported by the chitinous plate (*e*), together form the free front part of the lower lip which is grooved above; *f* and *e* are probably equivalent to submentum and mentum. The end-flaps (*c c*) are probably the modified paraglossae borne by the ligula, though Burmeister holds them to be labial palps.

Müller (p. 38) explains how these structures are disposed:—1. when feeding on pollen; 2. when sucking nectar; 3. when at rest.

1. *In order to feed on pollen* the fly stretches out the extensible proboscis¹, moving it, as may be necessary, straight forwards, upwards, or downwards, grasps with the two end-flaps, as with two hands tied together at the wrists, a little mass of pollen, rubs this down to separate grains by a rapid movement of the flaps, and passes the grains back by the same movement into the groove on the labium. In this groove lies the labrum, which is grooved below, and encloses the chitinous mandibular piece, the two being ready to seize the pollen. As soon as this is ground back by the end-flaps, the labrum and mandibular piece separate somewhat by means of their bases the parts immediately surrounding the mouth, seize the pollen now lying in the groove of the labium and thrust it back into the mouth, apparently by working against each other longitudinally. After a few seconds the first portion is swallowed, and the same series of actions is repeated. When the pollen-grains are united into long strings by elastic threads, as in *Oenothera*, an action of the fore-legs, alternating with the proboscis movements just described, is necessary to free the pollen-grains from the threads. After the fly has torn away a little mass of pollen from the anther, it brings up the fore-feet to its mouth, standing meanwhile on the mid- and hind-legs: then taking the cord of elastic threads between the fore-feet, and quickly rubbing them together as if washing its hands, it tears the threads asunder, and clears them off the proboscis and legs. Sometimes, to free the end-flaps from adhering pollen, it takes the proboscis in its fore-feet and draws them along from back to front. A remarkable peculiarity of the flaps, clearly shown in Fig. 73, makes them admirably adapted for seizing pollen, grinding it down, and passing it backwards. This consists in the fact that their apposed surfaces are closely and evenly beset with parallel chitinous ridges, by which the pollen-grains are easily held fast and pushed into the lower end of the labial groove.

The peculiarity in question is undoubtedly an adaptation to feeding on pollen, for it obviously facilitates this, and it is well marked in precisely those families of which the members visit flowers to obtain both pollen and nectar (*Syrphidae*, *Muscidae*, *Stratiomyidae*), while it is absent in flies which feed only on nectar (*Bombyliidae*, *Empidae*, and *Conopidae*), as well as in gnats, which also are purely suctorial. The gad-flies (*Tabanidae*) have never been seen eating pollen, although their end-flaps possess similar chitinous ridges. Since, however, a few species (e. g. *Tabanus micans* and *T. luridus*) are often found on flowers, it is not improbable that they too are pollen-eaters.

2. *In order to suck nectar* a hover-fly apposes the grooved labrum (Fig. 73, 1, *h*) and chitinous mandibular piece (*i*) to form a tube, which is then bent down so as

¹ In *Eristalis tenax*, which attains a length of 15 mm., the outstretched proboscis is 7 to 8 mm. long. In *E. arbustorum*, which is 10 mm. long, the proboscis is 4 to 5 mm. long.

to be enclosed in the labial groove. The insect now uses the end-flaps in one of two ways: it either folds them together (as in Fig. 73, 1) while the membranous middle piece (*f*) of the labium is so far retracted that the suctorial apparatus enclosed in the labial groove protrudes in front of the flaps and dips into the fluid to be sucked; or else it spreads out and flattens the flaps so that their rough inner surfaces are closely applied to the flower, and the tip of the suctorial apparatus protrudes from the end of the labial groove. Flies with swollen, cushioned-shaped flaps (*Syrphus balteatus*, Fig. 75) usually behave in the latter way, those with long, narrow flaps (*Rhingia*, Fig. 74) invariably adopt the former. Both pollen-grains and fluid which have been carried into the tube formed by the chitinous pieces *h* and *i*, are aided in their passage to the mouth by dilatation of the sucking stomach. The laciniae and maxillary palps seem to play no part either in sucking or in feeding on pollen, and hence must be looked upon as useless appendages.

3. In order to bring the proboscis into the sheltered rest position the fly draws the musculo-membranous basal piece (*g*) backwards and downwards, the labrum, mandibular piece, maxillae, and maxillary palps fold together above, and the very contractile middle piece (*f*) is completely retracted, being thrown into a few membranous folds at the lowest part of the proboscis. The chitinous plate (*e*) and the end-flaps (*c*) simultaneously fold upwards and forwards, and the complicated proboscis (equally adapted for pollen-eating and nectar-sucking) now lies so deeply hidden in the deep cavity underneath the snout-like prolongation of the head (Fig. 72, 1, 2, *m*), that at most the end-flaps protrude a little (Fig. 72, 1). If the head is now examined from below (Fig. 72, 2), nothing will be seen in the cavity but the end-flaps (*c c'*), and beneath these the upper part of the chitinous plate (*e*), of which the lower part lies in the folds of skin belonging to the contractile part of the proboscis.

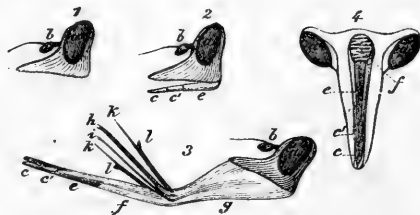


FIG. 74. Proboscis of *Rhingia rostrata* (after Herm. Müller). (1) Head with completely retracted proboscis; seen from the side. (2) The same, at the moment the proboscis begins to unfold. (3) The same, with proboscis completely extended. (4) Head with completely retracted proboscis; seen from below; (enlarged twice as much as (1), (2), and (3).) References as in Fig. 72.

An advance on these adaptations, furthering convenience in eating pollen, enabling more deeply seated nectar to be sucked, and rendering complete shelter of the proboscis under the head possible, would result from the greater elongation of this organ, with concomitant development of the snout-like prolongation of the head. Such a state of things finds its fullest expression in *Rhingia* (Fig. 74), where the proboscis (11–12 mm. long) exceeds the whole body (10 mm.) in length, being unsurpassed in this respect by any indigenous fly¹.

This hover-fly takes a foremost place among our native Diptera, not only in regard to the length of its proboscis, but also with reference to its power of detecting deeply hidden nectar. There is scarcely a single flower with nectar it can reach

¹ *Bombylius discolor* *Mik.* alone equals it in length of proboscis: *Bombylius major* *L.* approaches it (10 mm.).

that it does not discover and utilize. Even the deeply hidden nectar-receptacles of *Iris* are found and sucked by *Rhingia*. In anthophilous insects, the power to detect hidden nectar increases *pari passu* with the structural adaptations for securing it. When Sprengel described flies as stupid insects, incapable of finding nectar which lay concealed, that statement applied to the great majority of short-tongued forms, but not at all to forms with long proboscides, such as *Syrphidae*, *Bombyliidae*, *Conopidae*, and *Empidae*.

Even in the *Syrphidae*, however, only a few species have acquired so highly specialized a proboscis as *Eristalis*: the great majority are in a much lower stage of adaptation, as shown in Fig. 75. The labium is much shorter, its extensible middle joint is wanting, the terminal flaps are swollen and cushion-shaped, and there is a corresponding diminution in intellectual power in regard to the spoliation of flowers. This is indicated by the large amount of variation in the length of the proboscis, as follows:—

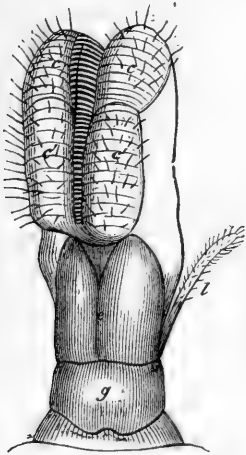


FIG. 75. *Proboscis of Syrphus balteatus*, Deg.: seen from below (after Herm. Müller). References as in Fig. 73.

	mm.
<i>Syrphus balteatus</i>	2
„ <i>ribesii</i>	3-4
<i>Eristalis arbustorum</i>	4-5
<i>Helophilus trivittatus</i>	6-7
<i>Eristalis tenax</i>	7-8
<i>Volucella bombylans</i>	8
<i>Rhingia rostrata</i>	11-12

With reference to this dissimilarity in the length of the proboscis of species belonging to the same family, Loew very rightly remarks (*‘Blumenbesuch,’* II, p. 117) that it is necessary to test each *Syrphid* as regards its stage of adaptation. For this, however, the observations so far recorded are insufficient. Loew thinks that there may possibly be a continuous series of transitional stages between purely allotropic forms and well-marked hemitropic ones.

Loew (*‘Blumenbesuch,’* II, p. 116) calls attention to the fact that the more or less well-developed feathery of the antennae of some species is of importance for the transfer of pollen from flower to flower. It is especially well marked in the genus *Volucella*. The curved pendent dorsal brush of the antennae is more than 2 mm. long in *V. bombylans*, while the lateral branches are about 1 mm., and numerous pollen-grains are not infrequently found adhering to the dense feathery hairs. As Loew further remarks, the dorsal brush forms the most prominent part of the head, so that the fly in alighting on flowers will—so far as the structure of these permits—in many cases deposit pollen-grains on the stigma. An equally well-developed feathery of the dorsal brush also occurs in *Sericomyia* and *Arctophila*, while in *Cheilosia* and *Eristalis* there are species with naked dorsal brush as well as others where it is feathery.

Loew further regards the hairs below the eyes of many *Syrphidae* (*Leucozona*, *Volucella*, *Sericomyia*, *Arctophila*, *Eristalis*, and species of *Cheilosia*) as an adaptation

to pollen-transference. Perhaps, too (according to Loew), the extremely well-developed hairy covering of the eyes of numerous flower-visiting flies is a similar adaptation, although this 'character is also possessed by many species that do not visit flowers.

In observing hover-flies at work among flowers, the impression is forced on us that they delight in gaudy colours that are disagreeable to us. I observed that even artificial flowers fastened to a lady's hat exercised a powerful attraction on a medium-sized species of *Syrphus*, so that it persistently hovered in the air in front of the flower, now and then darting to the side, but soon again to return to its former position. Hermann Müller ('Befruchtung,' p. 278, note) describes the conduct of *Syrphus balteatus* Deg. when visiting the flowers of *Verbascum nigrum* as follows:— 'The behaviour of this beautifully coloured hover-fly clearly proved to me its well-developed colour-sense. I watched it for over a quarter of an hour from a very small distance, without disturbing it by my presence. It hovered for a considerable time (ten seconds or more) at the same spot in front of the beautiful flowers 6-10 cm. away, to all appearance absorbed in gazing at them; it then rapidly darted forwards, touched one of them for a moment, and immediately retreated. After these manoeuvres had been repeated a number of times, until the insect had gloated over the sight of the flower to satiety, it alighted upon a petal, seized the middle of a filament with the fore-legs, and its lower part with the hind-legs, and began to loosen and grind the pollen for itself by actively moving the flaps of the proboscis to and fro. After carrying on this operation for five to ten seconds or more, it worked for some seconds with its flaps among the club-shaped violet hairs of the filament, and then went to another stamen of the same flower, treating this similarly. It also licked and pollinated the stigma. After having fed sufficiently from a flower, it renewed the hovering and gazing already described.'

Müller also observed ('Fertilisation,' pp. 440 and 80) the similar visits of *Syritta pipiens* L. to *Veronica Beccabunga* L. and of *Eristalis intricarius* L. to *Caltha palustris* L. The delicate little *Syritta*, enjoying the sunshine, hovers in one place before the beautiful blue flowers of *Veronica Beccabunga*, approaches it backwards, and then hovers again, till suddenly with a fresh dart it settles on a blossom. The beautifully tinted hover-fly *Eristalis intricarius* when visiting the flowers of *Caltha* also shows very clearly the pleasure it takes in bright colours. Just as the male *Eristalis* is wont to hover in its love-sport above the female, so does this insect often poise itself for a considerable time over one of the golden-yellow flowers, suddenly darts down upon it to suck nectar or eat pollen, and then flies abruptly above another blossom, there to repeat the same conduct.

This noteworthy proclivity of hover-flies, which can be observed on all occasions, indicates that they possess marked preferences with regard to choice of flowers, and it is therefore intelligible that special 'hover-fly flowers' (see pp. 135-6) should have been evolved.

With regard to the visits of *Syrphidae* to flowers, I have shown ('Blütenbesucher,' II, p. 11) that though they are specially attracted by social flowers, they nevertheless seek with almost equal zest flowers with half-concealed or exposed nectar, and more rarely those with entirely concealed nectar, provided this is hidden at a level corresponding to their proboscis, which is usually of medium length. They also

readily visit pollen flowers, since pollen is an important food to them. As a rule they only frequent bee flowers and lepidopterid flowers for the purpose of stealing pollen.

From Loew's statistical investigations ('*Blumenbesuch*,' II, p. 120) it appears with regard to the visits to flowers of the more highly specialized flies (exclusive of Syrphidae, Conopidae, and Bombyliidae) that there is a noticeable increase in visits to pollen flowers, bee flowers, and lepidopterid flowers on the one hand, and a diminution in visits to flowers with slightly concealed or exposed nectar on the other hand.

The Syrphidae and Empidae in the Alps (H. Müller, '*Alpenblumen*,' p. 517) devote a not inconsiderable share of their visits to flowers with fully exposed nectar (**E**), but clearly prefer such as have the nectar partly or completely concealed (**EC**, **C**), and affect to a much greater extent social flowers (**S**), which afford a rich booty. Only a small proportion of their visits are paid to bee flowers, lepidopterid flowers, anemophilous flowers, and pollen flowers. Among the pollen-eating Syrphidae, however, a considerably larger proportion of visits is naturally paid to the latter than in the case of the Empidae, which only suck. Moreover, the preponderance of white and yellow flowers over the red and blue is almost exactly the same in both cases (about 70:30 %).

In the large family of Syrphidae the preference for red, violet, and blue colours increases with the length of the proboscis in the different species. Considering their marked proclivity to pollen-eating, it is natural that greater specialization should lead to increasing preference for social flowers, which yield rich supplies of both pollen and nectar at the same time. Only *Rhingia*, with a proboscis 11-12 mm. in length, makes any considerable use of its ability to despoil bee flowers and lepidopterid flowers.—'Of the families of Diptera besides Syrphidae,' continues Herm. Müller ('*Fertilisation*,' p. 41) in his description of the structure and use of the proboscis¹, 'the Muscidae, Stratiomyidae, Bombyliidae, Conopidae, and Empidae are of some importance in the pollination of flowers. The species of the first two families both suck nectar and devour pollen: those of the last three only suck nectar.

'The pollen-eating *Muscidae* and the *Stratiomyidae* have the same soft, cushion-shaped swelling of the end-flaps, and the same armature of chitinous ridges upon them, as the Syrphidae; and, in spite of some structural differences, they use their mouth-parts for feeding in the same way as hover-flies, and similarly retract them when at rest into a cavity below the head.

'The species of *Bombylius*, *Empis*, and the *Conopidae*, on the other hand, are purely suctorial. Their end-flaps are not provided with soft cushions beset by horny ridges, but are formed of stiff, chitinous plates, which only serve to guide the suctorial organ, nor can this be retracted into a cavity.

'We may therefore conclude that the power of withdrawing the proboscis into a cavity below the head is of advantage only as a protection for the pollen-feeding apparatus, and is an indirect adaptation to flower-food, as is the snout-like or

¹ A work by E. Becher, '*Zur Kenntnis der Mundteile der Dipteren*' (Denkschr. Akad. Wiss., Wien, xiv, 1882), throws doubts on many points in Müller's description (Loew, '*Blumenbesuch*,' II, p. 110, note 3). I have not been able to see this work.

beak-like prolongation of the head in Syrphidae, which is correlated with an enlargement of the cavity for receiving the proboscis.

‘Among purely suctorial flies, the species of *Empis* carry their thin, straight proboscis directed downwards, and prefer to use it in that position. They therefore chiefly resort to erect flowers, into which they can plunge this organ vertically downwards. If the flower is tubular, and so much elongated as to make it necessary, they thrust the whole head down into the tube, an action which its small size renders possible, even when the tube is tolerably narrow. The chitinous piece formed by coalescence of the mandibles is broadened (e.g. in *Empis tessellata*) into a sharp, lancet-shaped plate, which, guided by the elliptical end-flaps, is used for boring into juicy tissue, such as the inner wall of the spur in species of *Orchis*. Any considerable increase in length in a downwardly-directed proboscis is clearly impossible without the development of a joint.

‘In the *Conopidae*, when the proboscis, which is still carried downwards, is of considerable length, it is bent like a knee at its base or in the middle. In the latter case the distal part folds back into the proximal, like the blade of a pocket-knife, thus enabling the proboscis still to be carried in a downward position.

‘The species of *Bombylius*, on the other hand, carry their proboscis (which here also is too long to be carried downwards without folding) directed straight forwards, and permanently ready for action. They thus obviously save time, for, without settling, they are able to insert the proboscis into nectar-yielding flower-tubes as they hover in the air, flying rapidly from one blossom to another. In length of proboscis they rival *Rhingia*, for in *Bombylius major* this organ is 10 mm. long, and in *B. discolor* 11–12 mm. They also approximate to *Rhingia* in their powers of detecting deeply concealed nectar. The species of *Bombylius*, like those of *Empis*, are also able to bore into succulent tissues. For the labium and the labrum which it encloses are gutter-shaped, and together form a tube in which the bristle-like maxillae, with the broad, strong, and pointed mandibular piece, move backwards and forwards. The labrum itself is drawn out into a stiff and extremely fine point. All these piercing structures, held between the long, narrow end-flaps, can easily penetrate soft tissues. I have often seen species of *Bombylius* thrust their proboscis into nectarless flowers (e.g. *B. canescens* *Mik.* into *Hypericum perforatum*), and I imagine that here the boring-apparatus was being brought into action.

‘While, so far as I know, the species of *Bombylius* and the *Conopidae* seek only the juices of flowers, very many other anthophilous flies are in the habit at times of sucking all kinds of other fluids and damp substances, these often being of uncleanly nature. Species of *Eristalis*, for example, may often be seen feeding eagerly in gutters, and species of *Scatophaga* and *Lucilia* on dung. *Sarcophaga* licks putrid flesh with relish, and even *Volucella bombylans*, so common on flowers, I noticed (in May, 1860) feeding on a floating carcase, returning repeatedly to it when driven away.’

To this account by Hermann Müller, E. Loew (‘*Blumenbesuch*,’ II, pp. 111 et seq.) adds that the mode of life and the structure of the proboscis in the great family of the *Muscidae* are extremely varied. This investigator, who has studied with particular care the structure of the insect proboscis, states that, in addition to

numerous groups with a thick membranous proboscis and broad end-flaps, there are forms with a long proboscis projecting far forwards and pointed end-flaps. Muscidae of this sort are sometimes voracious blood-suckers, as for example *Stomoxys calcitrans*; others, such as the species of *Scatophaga*, which possess a similar proboscis, live upon excrement, but also suck flowers and kill other insects. The proboscis of flies is at least as complicated and efficient an apparatus as the suctorial tube of bees. Since the large majority of Muscidae possess a membranous, more or less thick and long proboscis provided with broad end-flaps, and adapted for feeding upon moist substances, whether of vegetable or animal nature, we can by no means regard the family as mainly anthophilous. The more regular flower visitors belong more or less exclusively to the following sub-families only:—*Phasineae*, *Ocypterineae*, *Gymnosomineae*, *Phanineae*, *Tachinineae*, *Dexineae*, some *Sarcophagineae* (*Onesia*, *Sarcophaga*), *Muscineae* (*Graphomyia*, *Calliphora*, *Lucilia*, *Cyrtoneura*), *Ulidineae* (*Ulidia*), *Anthomyiæ* (*Aricia*, *Spilogaster*, *Anthomyia*), *Scatophagineae*, *Trypetineae* (*Acidia*, *Trypeta*, *Urophora*, *Myopites*, *Oxyphera*, *Tephritis*), *Sepsineae*, *Chloropineae* (*Chlorops*), and some *Drosophilineae*; the visits to flowers that are paid by species belonging to the remaining twenty sub-families are scarcely worth mentioning. In the mouth-parts of individual flower-visiting species belonging to the great family of Muscidae indications are found of increased specialization in the selection of flowers (e.g. in *Prosenia*, *Myopites*, *Ensina*, and some species of *Tephritis*), but such cases are exceptional and by no means the rule. Taking the behaviour of the Muscidae in general, it appears that ability to pollinate with correlated bodily structure occurs quite irregularly in the individual sub-families, so that these insects must be regarded as allotropous flower visitors.

The same holds true for the *Empidæ* (op. cit., p. 113), which in their mode of life show a relationship to other predaceous flies (*Asilidae*, *Therevidæ*, *Leptidae*). The proboscis is sometimes short, sometimes elongated. It projects horizontally forwards (*Hybos*), or is curved back (*Rhamphomyia*), or is directed perpendicularly downwards (species of *Empis*). Species of *Rhamphomyia* and *Empis* appear as visitors of flowers that only suck and do not eat pollen, and the males of species of the latter genus suck nectar, while the females in addition feed by sucking other flies.

The bloodthirsty *Tabanidæ* possess a thick proboscis, often extended forwards, and distinguished from that of other blood-suckers by its broad end-flaps. In *Tabanus* it is once more the males which specially devote themselves to sucking flowers, while the females as a rule draw blood from horses and cattle. Here too there are in addition to forms that are exclusively blood-suckers (*Chrysops*, and others), individual genera (*Silvius*, *Pangonia*) of which the species (at least the males) are exclusively anthophilous.

The *Conopidæ* only suck nectar. The proboscis may be of considerable length (in *Occemyia*), enabling nectar-yielding *Papilionaceæ* (such as *Trifolium*) to be plundered. They confine themselves almost exclusively to flowers with completely concealed nectar. As they suck while holding firmly with their feet, social flowers are visited with marked preference.

Although the family of the *Bee-flies* (*Bombyliidæ*) includes short-tongued forms (*Lomatia*, *Anthrax*, *Argyromoeba*) with a decided preference for flowers with exposed

nectar, the species of *Bombylius*, *Systoechus*, and *Dischistus* are provided with a long proboscis, with which they suck nectar as they hover. With regard to the rapid movement of their wings, and their way of visiting flowers, the *Bombyliidae* may be compared with the *Sphingidae*, as well as with the emerald-green and azure-blue Brazilian bees of the genus *Euglossa*, and with humming-birds. The movements of their wings are so rapid that to our eyes they appear motionless. Although these insects effect pollination much like hawk-moths, and readily visit lepidopterid flowers, we have no special 'bee-fly flowers.' On the other hand, some of the lower flies (*Muscidae*, gnats), the stupidity and inconstancy of which in visiting flowers was long ago repeatedly commented upon by Sprengel ('*Entd. Geh.*'), and which do not possess the smallest degree of adaptation to flower-food, serve as the exclusive or almost exclusive agents of pollination for flowers specially adapted to them, such as 'nauseous flowers,' 'pitfall flowers,' 'deceptive flowers,' and so forth. (According to Loew, '*Blumenbesuch*,' II, pp. 114-15.)

This fact, says Herm. Müller ('*Wechselbeziehungen*,' p. 19), which at first appears very strange, is susceptible, on closer examination, of a simple explanation. The adaptations of insects to procuring flower-food are obviously conditioned by the degree of their dependence upon it, and by the keenness of competition for the spoil, so that the most constant and zealous flower visitors must naturally be the most likely to participate in the results of natural selection. On the other hand, exclusive adaptation of flowers to a narrow circle of visitors can only occur when (and it can occur the more easily the more) such visitors possess certain peculiarities differentiating them from all others and rendering flowers otherwise useless and inaccessible available to them only. Now carrion-, flesh-, and dung-flies, and other *Diptera* fond of waste products, have tastes unlike those of all other flower visitors, and in accordance with this flowers might readily be evolved, and as a matter of fact have been evolved, which exclusively or chiefly attract *Diptera* of this kind, while at the same time they repel other visitors, or at least most of them, by inducing disgust. The more highly specialized flies (*Bombyliidae*, *Empididae*, *Conopidae*, *Syrphidae*), on the other hand, confine themselves exclusively to flower-food, and are (in part) most zealous and intelligent flower visitors, admirably adapted by the possession of a long proboscis to get at even deeply concealed nectar. But in spite of this they do not possess a single peculiarity fitting them to plunder flowers, in which they are not surpassed by bees and *Lepidoptera*.

It is easy for the *Bombyliidae* to plunder flowers with nectar completely concealed at a moderate depth, and even from lepidopterid flowers with a tolerably long corolla-tube they can extract nectar as easily as the *Lepidoptera* themselves. Bee flowers are also much more readily accessible to them than to the other anthophilous *Diptera*, and are more frequently plundered by them. On the other hand, social flowers are much less convenient for sucking while hovering, and are consequently only very rarely visited by these insects. In the Alps they were never met with on anemophilous flowers, pollen flowers, and flowers with fully exposed nectar, and but rarely on flowers with nectar partially concealed. Their preference for red, violet, and blue, is so remarkable that they were observed on three times as many flowers of these colours as on white or yellow ones (Müller, '*Alpenblumen*,' pp. 515-17).

While, therefore, certain *Diptera*, especially *Syrphidae* and *Bombyliidae*, are found

to be highly specialized flower visitors, this is not the case with the lower Diptera—the Muscidae, gnats, and the like. The selection of flowers by these forms is generally irregular, inconstant, and erratic, so that Hermann Müller's observations differ considerably from those of E. Loew. According to my own investigations (op. cit.), short-tongued flies (Muscidae, and others) prefer flowers with exposed nectar, which is conveniently situated for them, to as great a degree as the short-tongued wasps, which stand on a similar level as regards adaptation to flower pollination. They too are attracted by conspicuous social flowers, especially those which are white or yellow. Half-concealed nectar is somewhat too deep for them, so that they pay but slight attention to flowers presenting it. In their other visits to flowers they confine themselves almost exclusively to stealing pollen.

Although among the *less specialized flies*—i. e. Diptera other than Bombyliidae, Conopidae, Syrphidae, and Empididae—there are some species, genera, and even branches of families that are very constant in their visits to flowers, e. g. among the *Dolichopidae*, *Stratiomyidae*, and especially the *Muscidae* (*Gonia*, *Ocypetera*, and *Prosenia*, with a much elongated proboscis), they are nevertheless insignificant in number and importance, compared with the hundreds of more stupid species with shorter proboscis. Among these Diptera that are less capable of pollinating flowers, the visits paid in the Alps to white and yellow blossoms are far more numerous than those to red, violet, and blue ones. But here again in comparing families or sub-families that are constant or inconstant in flower selection, and possess respectively a long or a short proboscis, it becomes plainly evident that with increasing capacity for flower pollination the preference for red, blue, and violet becomes more and more marked, while the liking for flowers with exposed nectar correspondingly diminishes (H. Müller, 'Alpenblumen,' pp. 515, 518).

D. Beetles (Coleoptera).

The Coleoptera exhibit (Herm. Müller, 'Fertilisation,' pp. 32–6) unequivocal adaptations to procuring flower-food. They are of importance for pollination since many species belonging to widely different families seek out flower-food in addition to other nourishment, and a still greater number are entirely anthophilous. Although none of our native plants are pollinated by beetles exclusively or even chiefly, yet these insects largely co-operate in the discharge of this office for many flowers. The numerous species of the genus *Meligethes* are so small that they can creep into most flowers, and in many cases transfer pollen. On the other hand, beetles greatly damage many flowers by devouring the anthers and other structures.

In flowers with exposed nectar (*Umbelliferae*, *Cornus*, *Parnassia*), continues Herm. Müller, many species of beetles may be seen licking it; also in flowers with exerted stamens and nectar which though concealed is accessible to very short-tongued insects (*Rosiflorae*, *Compositae*), beetles may be seen licking up nectar, devouring pollen or anthers, or even gnawing the petals and pistils. In flowers with conspicuous anthers, and either devoid of nectar or with this too deeply concealed (*Ranunculaceae*, *Plantago*), beetles feed upon the pollen, the anthers, and other soft structures. Flowers which afford shelter from wind and rain (*Campanula*, *Digitalis*) are also visited by beetles, which devour the pollen and soft tissues. In more

southern regions, according to Delpino ('Ult.oss.,' Atti Soc. ital. sc. nat., Milano, xi, 1868, xii, 1869), some flowers of this kind, e.g. *Magnolia*, are even exclusively adapted to pollination by beetles (*Cetonia*). Lastly, we sometimes find beetles upon flowers which offer none of the advantages above described, but only seem to allure by means of their bright colours: thus, for instance, *Cryptocephalus sericeus* and *C. Moraei* are often attracted by the vivid yellow blossoms of *Genista tinctoria*.

A review of the habits of beetles which visit flowers, and of the families to which they belong, shows continuous gradations from forms which never visit flowers to those which partly nourish themselves on flower-food, and finally to those which entirely depend upon it. This shows clearly that insects which were not originally anthophilous gradually became more and more habituated to flower-food, and only acquired structural adaptations fitting them to successfully obtain such food after coming to depend upon it entirely.

But few beetle larvae maintain themselves on flower-food (*Helodes aucta*, *Meligethes*). Other beetles, which as larvae ravage flowers, e.g. the apple-blossom weevil (*Anthonomus pomorum*), leave them at once on attaining to the perfect state. Among beetles which are anthophilous when adult, the larvae may be carnivorous (*Telephorus*, *Trichodes*, *Coccinella*), or may devour putrid animal matter (*Dermestidae*), or feed on living or decaying vegetable matter (*Buprestidae*, *Cerambycidae*, *Elateridae*, *Chrysomelidae*, *Curculionidae*, *Cistela*, *Lagria*, *Mordellidae*, *Lamellicornia*).

Of the carnivorous larvae mentioned, most species of *Coccinella* and *Telephorus* retain their predaceous habits when adult, but some (*Coccinella septempunctata*, *punctata*, and *mutabilis*; *Telephorus fuscus* and *melanurus*; and others), though they do not disdain flesh altogether, resort more or less to flowers, while the adult *Trichodes* entirely abandons the carnivorous habit and becomes purely anthophilous.

Of the larvae mentioned which feed upon putrefying animal matter, *Dermestes* retains this habit when adult, never visiting flowers, and this is also sometimes the case with *Anthrenus* and *Attagenus*. But the same species of the last two genera, which under favourable circumstances (e.g. in neglected zoological collections) may feed for many generations on animal matter, without even leaving the cases whose contents they are destroying, in other circumstances may be found by hundreds upon flowers, busily feeding upon pollen and nectar.

The most perfect series of gradations in anthophily is found, however, in those families where the larvae feed upon vegetable matter, as the following selection will show.—No species of *Bostrichidae* is to be found on flowers: of *Curculionidae* only a very small minority resort exceptionally to flowers, either those of the same plants on which they have developed (*Gymnetron campanulae*, *Larinus Jaceae* and *senilis*¹), or of other plants on which exposed nectar is to be found (e.g. *Otiorynchus picipes* on *Cornus*, species of *Apion* on *Adoxa* and *Chrysosplenium*): the *Chrysomelidae*,

¹ Herm. Müller found larvae and pupae of *Larinus senilis* F. at Mühlberg in Thuringia at the base of the capitula of *Carlina acaulis*, and the perfect insect on the leaves, and now and then on the flowers of the same plant.

besides presenting the two stages exemplified in Curculionidae¹, possess species which in the perfect state are either mainly or exclusively anthophilous, either feeding on nectar (e.g. *Clythra scopolina*) or on the soft parts of flowers (e.g. *Cryptocephalus sericeus*). But even in Chrysomelidae, the anthophilous species constitute but a small part of the whole family. The same holds good among *Lamellicornia* for *Melolontha L.* and *Cetonia L.*, the anthophilous species of which either feed upon foliage-leaves, only occasionally resorting to flowers, where they devour all the soft parts indiscriminately (*Phyllopertha horticola*), or else subsist chiefly (*Hoplia philanthus*, *Cetonia*) or exclusively (*Trichius fasciatus*) on flower-food. Of *Cerambycidae* and *Elateridae* at least half our native species resort to flowers, some only incidentally (*Rhagium*, *Clytus arietis*, *Diacanthus aeneus*), but the greater number exclusively. Finally, among the *Mordellidae*, *Oedemeridae*, *Malachiidae*, and other families, all the species live solely on flower-food when they are adult.

To Müller's account I would add two observations, which are interesting because they show that even the most markedly predaceous beetles may occasionally

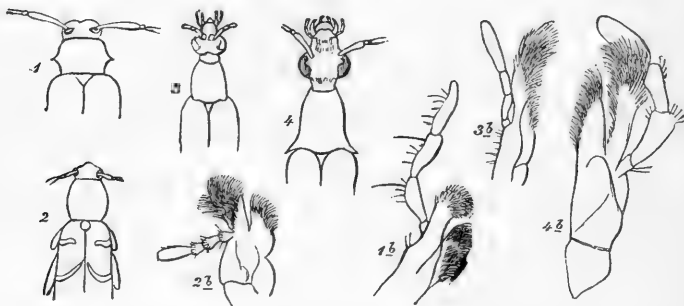


FIG. 76. *The Adaptations of longicorn beetles to feeding on nectar* (after Herm. Müller). (1) *Leipopus nebulosus L.*, which never visits flowers. Head turned downwards, no neck-like constriction behind the eyes, prothorax broad. The hairs on the maxillary lobes (1 b) are short and bristly. (2) *Clytus arietis L.*, which occasionally visits the flowers of Umbelliferae and Rosaceae. Head turned less sharply downwards, post-ocular region less broad, prothorax longer and narrower, outer lobe (galea) of maxilla (2 b) beset with longer hairs. (3) *Leptura livida F.*, which is exclusively anthophilous, visiting Umbelliferae, Rosiflorae, Compositae, Convolvulus, and so forth. Head forwardly elongated and turned to the front, a post-ocular constriction, outer (galea) and inner (lacinia) lobes of the maxilla (3 b) with long hairs. (4) *Strangalia attenuata L.*, which is exclusively anthophilous, and able to suck nectar from the corollatubes (4-6 mm. long) of *Knautia arvensis*. Characters as in the preceding species, but the prothorax is still longer and more tapering in front, and both lobes of the maxilla (4 b) possess long brushes of hair.

visit flowers, and sometimes do not disdain flower-food. In July, 1892, I saw ('*Blumen und Insekten auf den nordfries. Ins.*,' p. 165), upon the island of Föhr, *Carabus cancellatus* devouring the flowers of *Thymus Serpyllum*. It held the plant so fast with its mandibles that I was able to move both together for a short distance. Near Friedrichroda in Thuringia I saw during July, 1894 (at 9 p.m.), *Carabus*

¹ *Helodes phellandrii*, for example, lives as a larva in the hollow stems, and sometimes as an adult on the flowers of *Phellandrium aquaticum*. *Cassida murraea* lives in the larval state on the leaves of *Pulicaria dysenterica*, and sometimes when adult on the flowers of the same plant. *Crioceris punctata* lives in the larval state on *Asparagus*, and as a beetle sometimes feeds on the nectar of Umbellifers.

violaceous creeping about the inflorescences of an Umbellifer (*Aegopodium Podagraria*), obviously pursuing other visitors.

Considering the small importance of beetles with regard to pollination, continues Herm. Müller (op. cit., p. 34), it is scarcely worth while to compare all the anthophilous species, genera, and families with their nearest non-anthophilous relatives in order to discover any possible adaptations to flowers. It will be sufficient to investigate one family—the *Cerambycidae*—with this object.

One of the chief groups of this family, the *Lepturidae*, includes our native genera *Rhamnusium*, *Rhagium*, *Toxotus*, *Pachyta*, *Strangalia*, *Leptura*, and *Grammoptera*. The large majority of species belonging to these genera are exclusively anthophilous when adult, except those of *Rhamnusium*, which are never seen upon flowers, but only on willows and poplars. The species of *Rhagium* are found chiefly on fallen wood, but now and then on flowers; those of *Toxotus* mostly occur on flowers, more rarely on shrubs; and the species of the four remaining genera confine themselves entirely to flowers. *Pari passu* with increasing predilection for flower-food are developed those peculiarities in bodily structure which distinguish *Lepturidae* from other *Cerambycidae*, and which enable them to feed on exposed or more deeply seated nectar. The characters in question are: elongation of the head forward; a neck-like constriction behind the eyes, giving the power of directing the mouth to the front; elongation and anterior narrowing of the prothorax; and the development upon the lobes of the maxilla of hairs used to lick up nectar (Fig. 76).

All these characters present a complete series of adaptational stages, from those *Cerambycidae* which never visit flowers, and those which can only lick tolerably exposed nectar, up to *Strangalia attenuata*, which is able to extract nectar from the bottom of the corolla-tubes of *Knautia arvensis* that are 4–6 mm. long.

In concluding his account Herm. Müller remarks that, 'although the Coleoptera are of little importance for the pollination of our native flowers, they are nevertheless of special interest. This is because they show very clearly the first beginnings of insect anthophily, and the early adaptations correlated therewith. We see that among the most diverse coleopterous families, of which the members vary greatly as to their diet, individual species have first partly and then entirely accustomed themselves to flower-food, with the result that variations favourable to this habit have been naturally selected. Transition to the anthophilous habit must in some cases have taken place long ago, in other cases more recently, for we find on the one hand that sufficient time has elapsed for the evolution of anthophilous genera and families—by adaptational divergence—while on the other hand we find anthophilous species side by side with sister species that have no taste for flower-food.'

These details of coleopterous structure as described and luminously expounded by Hermann Müller, apply only to our indigenous species. As he himself remarks ('Fertilisation,' p. 433, note), 'Some tropical and sub-tropical beetles present much more thorough adaptation to flower-food. Thus, in a species of *Nemognatha*, which my brother Fritz Müller observed sucking flowers of *Convolvulus* at Itajaky [in South Brazil], the outer maxillary lobes (galeae) are modified into sharp grooved bristles (12 mm. long), which when apposed form a suctorial tube like the proboscis

of a butterfly, but of course incapable of being rolled up.' H. Hagen (Proc. Soc. Nat. Hist., Boston, xx, 1880, pp. 429-30) states that twenty-six species of *Nemognatha* with thread-like maxillae are known in America.

These species, as well as perhaps the foreign genus *Chauliognathus* *Hentz.* (Telephoridae), with extraordinarily elongated stalk-like maxillae, and possibly also some of the Eucharidae and Hopliidae, are placed by Loew among the *hemitropous* flower visitors. All our indigenous beetles are allotropous or dystropous.

Loew describes as *allotropous* ('Blumenbesuch,' II, p. 140):—

(a) Constant flower visitors with distinct structural adaptations for procuring sap, and heterobiotic larvae (Lepturidae, Oedemeridae, some Cantharidae and Lycidae).

(b) Constant flower visitors with indistinct or no structural adaptations for procuring sap, and heterobiotic larvae (Melyridae, Mordellidae, some Cistelidae, Cleridae, Buprestidae, and Elateridae).

(c) Flower visitors evolved from dystropous forms, with distinct structural adaptations for procuring sap, and with heterobiotic larvae (Cetoniariae, Trichiariae).

(d) Constant flower visitors with homobiotic larvae (Phalacridae, some Nitidulidae).

(e) Occasional flower visitors, of primarily carnivorous habit (some Cleridae, Coccinellidae, and Staphylinidae).

(f) Occasional flower visitors, of primarily saprophagous or xylophagous habit (some Dermestidae and Ptinidae).

According to Loew (op. cit.) the following are *dystropous*:—

(a) Curculionidae, with proboscis.

(b) Lamellicornia, with toothed maxillary lobes (Melolonthidae).

(c) Chrysomelidae, with pronounced homobiosis of larvae and adults.

According to my statistical investigations ('Blütenbesucher,' II, p. 11), the allotropous beetles occur in by far the greatest abundance on flowers with exposed nectar, which are best adapted to their short proboscis, but they also visit flowers with half-concealed nectar. The more deeply placed nectar of the other classes of flowers is beyond their reach. Their marked preference for pollen induces them not only to visit pollen flowers diligently, but also to devour this sort of food in the blossoms of other classes, especially in social flowers, where it is especially abundant. Loew's results ('Blumenbesuch,' II, p. 144) agree with this.—Flowers with completely concealed nectar, bee flowers, and lepidopterid flowers, are visited only to a small extent by such unskilled flower guests as beetles, and such visits are as a rule merely destructive. Pollen flowers and anemophilous flowers are much more frequently sought out, as they afford welcome food to many beetles. Insects of this order mostly affect flowers with exposed nectar and those which are social, the former on account of the accessibility of their nectar, and the latter because they are rich in pollen.

In the Alps (Müller, 'Alpenblumen,' p. 513) the visits of beetles to flowers are divided on the whole very impartially between the different groups, which is to be explained by the fact that many of them not only lick nectar or eat pollen, but also devour any delicate floral structures. But even among them there appears to be

a decided preference on the one hand for flowers with immediately visible nectar (E, EC), and on the other hand for social flowers (S), which are remarkably conspicuous and rich in booty. It is also apparent that among beetles, as generally among all insects at a low stage of adaptation (wasps, lower Diptera), the frequency of visits diminishes *pari passu* with the better concealment of nectar.

With regard to colour-preference among beetles, it is to be noted that they always like white and yellow flowers best. The opinion expressed by Hermann Müller ('Befruchtung,' p. 103) that beetles do not like dull yellow colours, but only seek out flowers of a brilliant yellow, was withdrawn by him later ('Weit. Beob.,' I, p. 305), because he found beetles visiting dull yellow flowers, an observation which was also confirmed by Loew ('Beiträge,' p. 28).

E. Other Insects that visit Flowers.

The Thripidae of the order **Thysanoptera** (or of the division of Orthoptera known as Physopoda) are easily distinguished from all other insects by their feet, which in all the species are devoid of claws and end in a large vesicle. The species of the genus Thrips barely attain at most a length of 1 mm., and their breadth is very much less than this, so that they can easily make their way into flowers. 'Probably,' says Hermann Müller ('Fertilisation,' p. 44), 'few of our indigenous flowers, if any, are altogether exempt from their occasional or frequent visits, and though these minute and extremely active little creatures certainly only convey pollen to stigmas by chance, yet on account of their great abundance their value for pollination must not be underrated. It must be almost impossible to keep out these guests when we try to exclude pollinating insects by placing nets over plants. They seek out both pollen and nectar, obtaining the former by seizing the individual pollen-grains and conveying them to the mouth by a pincer-like grasping movement of the horny mandibles. They obtain nectar by apposing the mandibles and maxillae, so as to form a short, conical suctorial apparatus. According to Westwood ("Introduction to the Modern Classification of Insects," II, p. 4) they avail themselves also of other plant juices. In all these respects their habits agree with those of the Diptera.'

Müller ('Fertilisation,' p. 45) supplements his account of the Thysanoptera by speaking of 'the young larvae of Meloë [an oil beetle], called by Kirby ("Monogr. Ap. Angl.," No. 11, Pl. xiv, Fig. 10), *Pediculus Melittae*, and by Dufour *Triungulinus*, which resemble the Thysanoptera in the activity of their movements, and in their minute size and slenderness, which permit entry into all flowers. Although these triungulin larvae visit flowers only to attach themselves as parasites to bees, they feed for the time on pollen and nectar, and not infrequently become dusted with the former, so that they play a part similar to, but even less important than, that of the Thysanoptera.'

Among the **Hemiptera** a few bugs (Hemiptera heteroptera Latr.) regularly visit flowers. The species of the genus Anthocoris (so named from their fondness for flowers) are fitted, according to Müller ('Fertilisation,' p. 31), by their small size to creep into and suck nectar from flowers of very various kind. Several Capsidae and Anthocoridae are found on flowers of Compositae, Umbelliferae, Cruciferae, Salix, and

so forth, not only sucking nectar, but—being dusted with pollen below—serving also as active pollinators. No structural adaptations to flower-food have, however, been seen, unless the small size of *Anthocoris* can be so regarded. The elongated proboscis, fitted for sucking nectar from tubular flowers, is just as characteristic of the other—and more numerous—land-bugs which never visit flowers, and it cannot therefore be regarded as an anthophilous adaptation. No flower has been observed as specially adapted to pollination by bugs, though such might be a quite conceivable possibility. Nor is a single species of flower known for the pollination of which bugs are of special importance, and accordingly the structure of their proboscis need not be considered.

Among the **Neuroptera** (net-winged insects), *Panorpa communis* has now and then been observed visiting flowers and sucking nectar. According to Müller ('Fertilisation,' p. 31) it is easy to satisfy oneself that it is really anthophilous, for it visits some flowers in which the nectar is somewhat deeply seated (e. g. *Polygonum Bistorta*, *Eupatorium cannabinum*, and so forth), plunging its long beak-shaped head into the various nectar receptacles. One might even be inclined to look upon the snout-like prolongation of the head as an adaptation to getting nectar from these flowers, were it not that the nearly related little wingless *Boreus hiemalis*, which never visits flowers, but lives in moss, possesses the same character, which may therefore be of different origin. Species of *Hemerobius*, *Sialis*, *Ascalaphus*, *Perla*, and others, are frequently met with upon the flowers of *Umbelliferae*. They bend their heads down to the fleshy disk-like nectaries and doubtless lick up their secretion. Small dragonflies (*Agrion*) sometimes settle on flowers (*Spiraea*), but apparently only to sun themselves.

Among **Orthoptera** only the earwig (*Forficula auricularia* and other species) has to be considered as a visitor of flowers (*Papaver*, *Tropaeolum*, *Trollius*, *Campanula*, *Compositae*, roses, pinks, peonies, and so forth), into which it creeps during the day, and feeds upon the softer parts at night.

Grasshoppers spring and fly about in quest of food on to various parts of plants, including the flowers.

Our indigenous **Orthoptera** do not show any anthophilous adaptations. But Darwin states that several New Zealand grasshoppers were observed by Mr. Swale to pollinate papilionaceous flowers (*Ann. Mag. Nat. Hist.*, London, ser. 3, ii, 1858, p. 461), but Hermann Müller remarks ('Fertilisation,' p. 30, note) that this seems very questionable and scarcely credible.

In South Brazil Fritz Müller observed a cockroach very similar to *Pseudomops laticornis* *Perty* to be a diligent visitor of flowers, occurring frequently, e.g. on the garden composite *Polymnia edulis*, apparently to feed on the nectar.

F. Stages of Adaptation in Insects which visit Flowers.

Though members of all insect orders visit our indigenous flowers, there are very great differences between these orders in respect of the number of anthophilous species and individuals, and also as to the degree of anthophily. Their importance for pollination of flowers and the amount of correlated adaptation are therefore very far from being the same.

Hermann Müller ('Alpenblumen,' p. 512) has distinguished *eight stages of adaptation among insects which visit flowers*:—

- I. Neuroptera, Orthoptera, Thysanoptera, Hemiptera.
- II. Coleoptera.
- III. Diptera which are little adapted to pollination. All the order except the families included in IV. Muscidae, Stratiomyidae, Dolichopidae, and so forth, are therefore placed here.
- IV. Diptera which are more or less well adapted to pollination: Bombyliidae, Conopidae, Empidae, Syrphidae.
- V. Wasps (Hymenoptera other than bees).
- VI. Bees with short proboscis (*Melitta Kirby*).
- VII. Bees with long proboscis (*Apis Kirby*).
- VIII. Lepidoptera.

Müller's division of Diptera into two groups (III and IV) is based on the following considerations ('Alpenblumen,' p. 513).—The families of Bombyliidae, Conopidae, Syrphidae, and Empidae are highly specialized in relation to flower-food, for well-marked intelligence and the possession of a long proboscis enable the species they include to secure nectar even when deeply hidden. All the species of the three first families are purely anthophilous when adult, while among Empidae the same thing is at least true for the genera *Empis* and *Rhamphomyia*. Some of the other families of Diptera—such as the Dolichopidae, the Stratiomyidae, and particularly the Muscidae—are also constant flower visitors as regards a larger or smaller proportion of their species, genera, and even sub-families, while among the Muscidae there are several forms of considerable intelligence and with a tolerably long proboscis, e.g. *Gonia*, *Ocyptera*, *Prosenia*. But as these forms are very limited in number and importance compared with the hundreds of their stupid short-tongued congeners, we are justified—when taking a broad survey—in grouping together the Bombyliidae, Conopidae, *Empis*, *Rhamphomyia*, and Syrphidae as Diptera more or less well adapted to pollination, and all the others as Diptera less adapted to it.

The division of Hymenoptera into wasps, short-tongued bees, and long-tongued bees (IV, V, VI), naturally follows from Müller's account of the structure and habits of these insects, as already given. He ('Alpenblumen,' p. 518) calls attention to the fact that wasps chiefly compete with beetles and short-tongued flies (p. 513), which he describes as being at the lowest stage of adaptation. In the same way he compares—as regards flower visits—the flies which are more specialized as pollinators with the unspecialized bees, for these display marked preference for flowers with partly or entirely concealed nectar. We find therefore that Hermann Müller partly anticipates the oecological classification that E. Loew has worked out in such an acute and admirable manner (see pp. 192–5).

C. Verhoeff ('Blumen und Insekten auf Norderney,' pp. 176–8) has reduced the stages of adaptation in insects to flower visits from eight to six. His groups IV, V, and VI entirely agree with the corresponding ones of Hermann Müller. In defining these stages of adaptation he pays special attention to the structure of the mouth-parts, the presence and character of a hairy covering, the size of the body, the activity during visits, and the frequency of these. Verhoeff distinguishes—

Stage I. Hemiptera, Neuroptera, Panorpidæ, Trichoptera, Dermaptera, and part of the Coleoptera. The mouth-parts and hairy covering do not show any distinct adaptations to flowers: the activity of the visits is very slight and their number very small.

Stage II. Many Coleoptera, Diptera, Orthorrhapha (except Empidæ and Bombyliidæ), Muscidæ acalyptratae; Phytophaga, Entomophaga, and Formicidæ among Hymenoptera. Here again distinct adaptations of mouth-parts and hairy covering are wanting, but visits are more numerous and their activity is markedly greater.

Stage III. Fossores, Chrysididæ, and Diploptera among Hymenoptera; Empidæ, Bombyliidæ, Syrphidæ, Conopidæ, and Muscidæ calyptratae among Diptera; also a few Coleoptera. The mouth-parts or hairy covering show more or less distinct adaptation to the flowers sought out by these insects. All are regular flower visitors.

Stage IV. Short-tongued Anthophila (bees with unspecialized labial palps). Not only are the mouth-parts—and usually the hairy covering as well—thoroughly adapted to flowers, but adults as well as larvae are dependent on flowers to such an extent that they could not live without them. They are not only regular, but also very energetic agents of pollination.

Stage V. Long-tongued Anthophila (bees with specialized labial palps). The mouth-parts are greatly elongated and the hairy covering usually very well developed. These insects are larger as a rule than bees with unspecialized labial palps. Owing to various improvements of the collecting-apparatus, their visits are made more rapidly, being at the same time more productive for themselves, and more beneficial to the flowers. The number and activity of visits reach a maximum. Adults and larvae are necessarily entirely dependent upon flowers.

Stage VI. Lepidoptera. Those which are regular flower visitors are distinguished by the possession of a more or less conspicuously long proboscis that can be rolled up. The adults are dependent upon flowers so far as they partake of nourishment of any kind. Since they take no care of their offspring their activity in visiting flowers is much less than that of the two preceding stages, and they have about the same value for pollination as Stage III. They are very important for flowers with long and narrow tubes, to which the proportions of their proboscis correspond. This organ must have become highly specialized at an early period of the earth's history, for transitional forms between Lepidoptera and their relatives the Trichoptera do not now exist.

The value as regards pollination of Verhoeff's six stages of adaptation is as follows:—I, II, III, VI, IV, V. This classification into stages is undoubtedly of great value, and in many ways agrees very closely with the actual facts. Yet it is to be remarked that the 'regular flower visitors' of Stage VI, including the hawk-moths (Sphingidæ), are at a much higher level as regards adaptation to flower pollination than Verhoeff supposes.

The classification of insects that visit flowers given by E. Loew appears to me to correspond more accurately with nature than that of Verhoeff ('Beob. ü. d.

Blumenbesuch v. Insekten a. Freilandpfl. d. bot. Gart. zu Berlin,' Jahrb. kgl. bot. Gart. zu Berlin, iii, 1884; iv, 1886: 'Beiträge zur blütenbiol. Statistik,' Verh. bot. Ver., Berlin, xxxi, 1890: 'Blütenbiol. Floristik,' pp. 386-8, Stuttgart, 1894). Loew's scheme has also been used by MacLeod and by Heinsius for statistical observations, and I myself have employed it in several investigations relating to the statistics of flower pollination, during which the conclusion has more and more forced itself on me that Loew has adopted the right method, though some change may be necessary in certain details.

Loew's first group—Allotropous Insects—includes Stage I and part of Stage II of Verhoeff's classification. To the second group—Hemitropous Insects—belong Verhoeff's Stages IV, III, and VI. The third group—the Eutropous Insects—corresponds to Verhoeff's Stage V, with a small part of Stage VI. The last of the groups established by Loew—Dystropous Insects—includes species which were not taken into consideration by Verhoeff.

Loew's stages of adaptation of insects to flower visits are defined as follows:—

I. Allotropous Insects. *Unequally and only slightly adapted flower visitors of little value for pollination.* They either lack special structural characters adapting them to flower visits—except such as may be involved in the features common to the group—or if any adaptations of the kind exist they are incipient. In addition to flower-food the insects of this group also nourish themselves on a great variety of other substances (e.g. the social Vespidae, the blood-sucking Empidae, Tabanidae, and others), and some of them are destroyers of flowers (e.g. many beetles, species of Cephus, and others). Their movements while visiting flowers are mostly irregular, only attaining any constancy in the more highly adapted species. Flower forms corresponding to allotropous visitors are very sparingly developed, and by no means to be regarded as adaptations to such insects alone, though these display marked preference for flowers of the kind.

To this group belong:—

1. *Hymenoptera*. Short-tongued digging-wasps (Fossores) and ruby-wasps (Chrysididae), most of the true wasps (Diploptera, e.g. Vespa, Polistes), saw-flies (Tenthredinidae), and ichneumons (Ichneumonidae).

2. *Diptera*. Muscidae, Empidae, Tabanidae, Therevidae, Leptidae, Stratiomyidae, Dolichopidae, Bibionidae, and others.

3. *Coleoptera*. Dermestidae, Coccinellidae, Nitidulidae, Lamellicornia (in part), Melyridae, Cerambycidae, Lepturinae, Oedemeridae, and others—in fact most beetles, excepting such as are particularly hurtful to flowers.

4. *Neuroptera*, *Orthoptera*, and *Hemiptera*. Such of these as are occasional flower visitors.

II. Hemitropous Insects. *Partially adapted flower visitors of moderate value for pollination.* The adaptations to successful flower visits are always distinctly recognizable, but are much more feebly developed than in the following group. The movements while visiting flowers are skilled, but not so regular and constant as in Group III. Flower forms specially adapted to these insects are rare.

The following belong to the group:—

1. *Hymenoptera*. Long-tongued digging-wasps (Fossores, e.g. *Bembex*, *Ammophila*) and ruby-wasps (Chalcididae, e.g. *Parnopes*), the solitary true wasps (*Eumenidae*, e.g. *Eumenes*, *Odynerus*, and others), short-tongued bees (*Apidae*, e.g. *Andrena*, *Colletes*, *Dasygaster*, *Halictus*, *Panurgus*, *Prosopis*, and *Sphecodes*, to which also may be added *Camptopoeum*, *Dufourea*, *Halictoides*, *Melitta*, *Macropis*, *Nomia*, and *Panurginus*).

2. *Diptera*. *Conopidae*, *Syrphidae*, and *Bombyliidae*.

3. *Lepidoptera*. All except the hawk-moths (*Sphingidae*), which belong to the next group.

4. *Coleoptera*. Only a few exotic beetles such as *Nemognatha*.

III. Eutropous Insects. *Completely adapted flower visitors of the greatest value for pollination.* They possess habits and structural modifications which further in high degree their own ends in plundering flowers, while at the same time they unconsciously effect cross-pollination in the most effective manner. They conduct their visits to flowers with the greatest constancy and regularity of movements. Corresponding to them in the plant world is an extraordinary variety of flower adaptations that can only be explained with reference to the regularly occurring cross-pollination effected by their visits.

To this group belong:—

1. *Hymenoptera*. Long-tongued bees (*Apidae*—*Anthidium*, *Anthophora*=*Podalirius*, *Apis*, *Bombus*, *Ceratina*, *Chalicodoma*=*Megachile*, *Chelostoma*=*Eriades* in part, *Coelioxys*, *Crocisa*, *Diphysis*=*Trachusa*, *Eucera*, *Megachile*, *Melecta*, *Meliturga*, *Nomada*, *Osmia*, *Psithyrus*, *Saropoda*=*Podalirius* in part, *Systropha*, *Tetralonia*=*Eucera* (*Macrocera*), *Trypetes*=*Eriades* in part, *Xylocopa*, and also *Rophites*).

2. *Lepidoptera*. Hawk-moths (*Sphingidae*).

IV. Dystropous Insects. *Flower visitors not adapted to pollination.* They are either—as some beetles (*Chrysomelidae*, many *Lamellicornia*, *Curculionidae*, and others), and also earwigs (*Forficula*)—wholesale flower devastators which devour floral structures, or else their habits are detrimental to pollination, as in the case of creeping flower guests (ants, aphides, thrips). It consequently follows that flowers possess protective arrangements repelling their visits but no adaptations facilitating them. There have in particular been developed in flowers a series of structures serving to prevent the entry of these unbidden guests, which are mostly nectar-thieves.

Ants, which are described as dystropous by Loew, are not regarded as such by Verhoeff ('Bl. u. Ins. auf Norderney,' p. 169), but Loew ('Blütenbiol. Floristik,' p. 387, note) calls attention to the fact that Hermann Müller in his 'Alpenblumen' also described ants as either valueless or harmful (\pm) for flowers, and of forty-three ant-visits he observed thirty-four were dystropous.

Loew describes as **Pseudodystropy** the case in which, 'even in completely eutropous forms, adaptations may be secondarily acquired which render their owner a devastator of flowers under special circumstances.' A very well-known example is afforded by *Bombus mastrucatus*, which in the Alps gets at the nectar of many

species of flowers by biting them through. *Bombus terrester* also frequently plays the part of a nectar-thief (cf. pp. 116-17).

As already mentioned (see p. 66) Loew has proposed a classification of flowers corresponding to the allotropous, hemitropous, and eutropous groups of insects. Under *Allotropous Flowers* he places the classes An, Po, E, and EC—under *Hemitropous Flowers* the classes C and S—and under *Eutropous Flowers* the bee flowers (Hb), humble-bee flowers (Hh), and lepidopterid flowers (L). The statistical investigations in flower pollination made by Loew, as well as by MacLeod, Heinsius, and myself, show that there actually is a marked agreement between the corresponding groups of flowers and insects. But there is still a need of more numerous and more thorough special investigations to make quite clear the relations between the two sets of groups.

The four groups of flower guests established by Loew are connected with one another by intermediate stages and transitional forms. This classification leaves untouched those theoretical speculations which have reference to the genetic development of the various insects.

X. Methods of Research in Flower Pollination.

The statistical method introduced by Hermann Müller to determine the reciprocal dependence between flowers and insects, and more especially employed by him in his 'Alpenblumen' (pp. 477-525), does not count the individual visits of insects to a species of flower, but only the number of insect species which seek out a particular kind of plant. At first sight this method seems unreliable, if not quite worthless. As a matter of fact it cannot be denied that a disadvantage is involved, though it is one that can hardly be avoided, for it is almost impossible to count all the individual visits that a conspicuous flower receives during a considerable period of observation when the weather is fine, or to establish how many flowers are pollinated by a species of insect in a given time¹.

The value of a method must, however, be judged by its results. Those attained by this method, as employed first by Hermann Müller and afterwards by E. Loew, J. MacLeod, and myself, show that (to quote from Loew, 'Blumenbesuch,' II, p. 147) it has greater possibilities than any one possessing only a superficial knowledge of it would be inclined to believe. In particular the reproach that it must afford an inaccurate idea of the number of pollinators, because it counts the visits of species and not of individuals, is of no importance. This appears from the agreement which exists between the determinations of Müller and those of all subsequent observers regarding the numerical relation of visits—not the absolute values, of course, but their proportions in a series—and many of the sets of observations were made quite independently of one another.

¹ Professor F. Dahl, of Kiel, informs me that he has constructed an apparatus that automatically catches all the visitors of a flower or an inflorescence. This would make it possible not only to ascertain the number of insect species that visit flowers, but also the number of individuals visiting a flower within a given time. Meanwhile Prof. Dahl will make a communication with regard to this apparatus at the meeting of the Deutsche Zoologische Gesellschaft (1898) at Heidelberg. The trap described and figured by him in his memoir ('Vergleichende Untersuchungen über die Lebensweise wirbelloser Aasfresser,' SitzBer. Ak. Wiss., Berlin, 1896) is made on a similar principle.

The value of this method, continues Loew, lies also in the fact that it is not a purely statistical one, furnishing only averages, but specifically oecological, by which the behaviour of individual insects with regard to flowers can be quite as well established as the behaviour of a complete group. The method has afforded valuable proof of the general correctness of Müller's rule of colour-preference, i. e. that insects which are more perfectly adapted to pollination generally affect dark colours (blue, red, violet), while insects which are less specialized prefer light colours (white, yellow). And, lastly, it is proved that insects choose flowers in the series as they would be expected to from the structure and length of their suctorial apparatus, and the nature of their general bodily equipment, i. e. *those pollinators and flowers which theoretically appear to be adapted to one another, are the very ones which actually exert the most marked mutual attraction.* This proposition of Loew's ('Beiträge,' p. 15) was previously postulated by Müller, but was only proved by later statistics.

The two following conclusions embody the general results of the statistical investigations made by myself in accordance with this method ('Blütenbesucher,' II, p. 9).

1. *The more specialized a flower—i.e. the more complex its structural arrangements and the more deeply seated its nectar—the less are its insect visitors indiscriminately drawn from the entire insect fauna of a district, and the more do they belong to one or several similar species adapted to pollination.*

2. *The flatter and more superficial the position of the nectar, the more varied are the visitors in different regions, and the more are they indiscriminately drawn from the entire insect fauna of the region in question.*

MacLeod ('De bevruchting der bloemen door de insekten,' Verhandlingen van het eerste Nederlandsch Natuur- en Geneeskundig Congress, gehouden te Amsterdam, op 30 Sep.—1 Oct. 1887, Amsterdam, 1888) has tested Müller's method from a new point of view. This investigator (op. cit., pp. 83–90) proceeds from the idea that always and everywhere the degree to which any particular group of insects visits a particular class of flowers depends upon three factors, i. e.—1. On the *Choice of Flowers* by insects, or in other words, on the preference of insects for certain flowers. 2. On the *Composition of the Flora*, i. e. on the proportions in which the various classes of flowers are represented in a district. 3. On the *Time of Year*, by which quite different species of flowers are offered to visitors during different months.

The first of these three factors, according to MacLeod, is constant for similar flowers and similar insects, which must be determined by statistics. The two other factors are varying quantities which must be eliminated before we can attain to a constant result.

The *influence of the Time of Year* can easily be eliminated by separating from one another the observations for various months and regions, and considering them individually. MacLeod divides the summer half-year (in central Europe from the first of April to the first of October) into intervals of thirty days, and places the observations in so many series according to their date. Each result is therefore repeated as often as there are monthly series, so that the degree of reliability of each conclusion can be estimated. It may be assumed that the plants in flower during a particular period of thirty days remain much the same.

To eliminate the *influence of the Composition of the Flora* upon the choice made by insects, a standard must be found for the proportions in which the various flower classes are represented in the flora of each month. The mere numbers of species belonging to each class that are in flower would not be sufficient, for in this way small, inconspicuous blossoms which attract but few insects would have the same value given them as large, conspicuous forms, rich in nectar, and attracting many insects. The actual standard indicating the importance of each class seems rather to be the degree in which the seven flower classes are visited by *all* insects. The number of visits that each class of flower received depends upon (a) the number of flowers in bloom, (b) the number of individuals (frequency or rarity of species), (c) the abundance of nectar, (d) the size and colouring of the conspicuous parts, i. e. the totality of the means of attraction, *the physiognomic value of each class in the flower world*.

MacLeod estimates for the species of each individual flower class the percentages of insect visits observed during a given month, and thus reaches approximately the degree to which the flower class in question attracts insects as a whole, each group of insects being separately considered. If, for example (according to Hermann Müller's observations in the Alps), during the month of June, all the flowers in the Alps below the limit of trees receive 947 different visits, these—according to MacLeod's calculation—would be distributed as follows among the flower classes:—

		<i>Visits.</i>	<i>Per Cent.</i>
Class	An	25	2.6
	„ E	82	8.6
	„ EC	270	28.5
	„ C	137	14.4
	„ S	146	15.4
	„ H	200	21.1
	„ L	87	9.2
	Total	947	99.8

Of the 947 visits, 201 would be paid by allotropic Diptera (i. e. all the anthophilous flies except Syrphidae, Bombyliidae, and Conopidae). If these were equally attracted by the seven flower classes, the 201 visits would be divided between the classes in the same proportions as the 947 visits of insects collectively were divided. But—as the following table shows—the proportions are quite otherwise: the visits of allotropic Diptera are paid as follows:—

		<i>Visits.</i>	<i>Per Cent.</i>
Class	An	3	1.5
	„ E	40	20.0
	„ EC	82	41.0
	„ C	45	22.5
	„ S	27	13.5
	„ H	0	0.0
	„ L	4	2.0
	Total	201	100.5

From this table it appears, for example, that Class E attracts allotropic Diptera more than the other classes. The proportion (20 %) of visits of Diptera to this class of flowers is higher than the proportion (8.6 %) of visits of insects in general, from which it may be concluded that Class E possesses means of allurements by which allotropic flies are specially attracted. By comparing the table relating to a particular insect group with that for insects in general, it is therefore possible to determine—for a given month and district—the flower classes which the insect group in question prefers or avoids.

MacLeod has worked through on this method Müller's observations in the Alps and Loew's observations in the botanic gardens at Berlin, and has drawn up ten different series according to the month and place of observation, so that the choice of flower of each insect group could be determined ten times.

The clearness of MacLeod's method is enhanced by the fact that he gave a *graphic* representation of his results. For each month he erected upon a horizontal line—at equal distances from one another—seven ordinates 100 mm. long, corresponding to the flower classes, and then measured off on each ordinate a length representing the proportion in which the class in question was visited by insects in general. By connecting these points with one another, he obtained a broken line which he described as the *general insect line*. In similar fashion he then drew *special lines* for the individual insect groups, so that the choice of flowers made by the several groups could be seen at a glance. Wherever a special line runs above the general insect line, the corresponding insects must have a preference for the particular flower class, and, conversely, the deeper a special line sinks below the general insect line, the greater is the repugnance manifested by the particular insect group towards the flower class indicated. To be of any value this graphic method must give *constant* results, and must therefore yield *the same result* for the same insect group and the same flower class, in each of the ten series of observations collated by MacLeod. Such uniformity obtains for the following cases:—

1. *Beetles* show a constant preference for An and E, while C, H, and L are the most repugnant to them.
2. *Allotropic Diptera* prefer E, and always reject H.
3. *Hemitropic Diptera* consistently prefer EC, and reject H.
4. *Short-tongued Bees* always avoid H.
5. *Long-tongued Bees* avoid E and S, and consistently prefer H.
6. *Lepidoptera* consistently prefer L, and reject E.

Although in other cases there was no agreement between the ten series of observations collated by MacLeod, it was demonstrated that the groups of flowers and insects are not homogeneous. In those cases where, on Müller's theory, strong preference or the opposite could be inferred of certain visitors in regard to certain flower classes, reasoning from the structure of the insects and of the flowers they visit, MacLeod's results were constant.

By this graphic method relations can be recognized which, although theoretically probable, were not deduced by the older ways of dealing with statistics, e.g. the preference of Lepidoptera for lepidopterid flowers comes out very clearly. MacLeod's method would furnish still more reliable results by taking smaller

periods of time, by still further dividing the insect groups, and by increasing the number of observations.

The first of MacLeod's graphic tables is reproduced, where each ordinate represents one of the seven flower classes (*An*, *E*, *EC*, *C*, *S*, *H*, *L*), while *abcdefg* is the *general insect line* for the month of June in the Alps—below the limit of trees—and *αβγδεζη* is the *Diptera line*.

For complete understanding of the law regulating the visits of insects to flowers the statistical observations that have hitherto been made in flower pollination are not sufficient, and full knowledge of this law will only become possible when numerous investigators take part in the work. Besides which many other related matters require more thorough study, e.g. the determination of the distribution of the sexes in different districts, the mechanisms of many flowers, and so forth. These problems, however, cannot be solved till such investigations have been systematically made in as many small, well-defined areas as possible.

When only occasional observations are made on flower pollination, it will appear as if insect visits were often very rare, even in the case of the larger and more conspicuous flowers. As a matter of fact we cannot calculate on seeing numerous insects visiting flowers in rainy or even dull weather, or in strong wind, and under such circumstances only occasional stragglers will be noticed. Even in warm, quiet weather there is frequently no abundance of flower guests to be

seen, and it then becomes necessary to patiently stay in one place and not wander aimlessly about. 'One must not be annoyed,' says the great Sprengel ('Entd. Geh.,' p. 23), 'at having to spend a long time near a flowering plant, and at having often to repeat the same observations on any species of flower, for it is not always visited forthwith by the particular insect which is designed to fertilize it.' As a rule patience will be rewarded, the proper insects putting in an appearance at last, even when the plant under observation stands alone. In the study of flower pollination it is necessary always and everywhere to be ready at a moment's notice to make observations. It should therefore be a rule never to go out without apparatus for capturing insects, and always to carry about cases for preserving captured specimens. Immediately after the sun has dried up the dews of night from the flowers the insects come forth from their night's quarters to make their visits, and the student of flower pollination

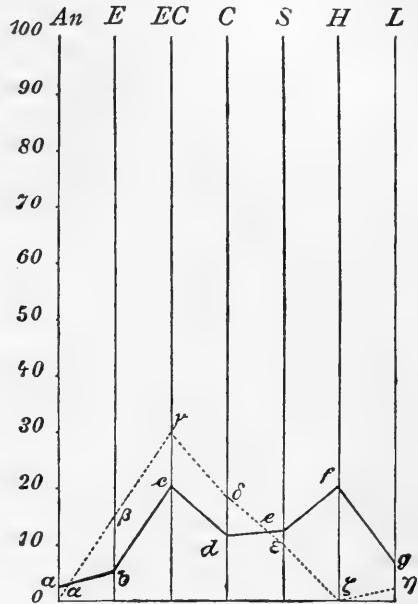


FIG. 77. Graphic representation of the visits of Diptera to various classes of flowers in the month of June (after J. MacLeod), reduced one-fourth. *abcde*fg, general insect line for the month of June in the Alps below the limit of trees; *αβγδεζη*, Diptera line. [The symbols for the flower classes used in this translation have been substituted for *P*, *A*, *AB*, *B*, *B'*, *H*, *F* employed by MacLeod.—Tr.]

must then be already prepared to make observations. It is in the early morning that insects are to be seen in abundance on many flowers, which later on seem dead and empty, since their mechanism for securing pollination has been put in action, and they have been plundered of their insect food. Sprengel says ('Entd. Geh.,' p. 23), 'It is especially the midday hours—when the sun high up in the unclouded heavens makes it warm or even hot—which are the time for making diligent observation. The day flowers then appear in their greatest beauty, and with all their charms tempt insects to visit them, and at this time their fertilization can the more readily be effected because the pollen of such anthers as are exposed to the air is quite dry. But it is precisely during these hours that insects—liking as much heat as possible—are most active in and upon the flowers, their aim being to gorge themselves with nectar, while at the same time they fulfil the design of Nature by effecting fertilization. In the realm of Flora, whose wisdom is no less admirable than her beauty, wonderful things take place at this time, of which the chamber-botanist—who is meanwhile busy with his breakfast—has not the faintest idea.'

Hermann Müller ('Alpenblumen,' p. 547) makes the following remarks about the visits of insects to flowers in the Alps.—'While in still weather and warm sunshine there is usually an abundance of insects visiting flowers, corresponding to their profusion, a cool breath of air is often sufficient to drive away most of the floral guests—especially the *Lepidoptera*—into their hiding-places. On the other hand, when calm, sunny weather suddenly returns after a few cold and windy days of fog and rain, increased activity is seen among the insects which fertilize flowers. The longer they have had to remain hungry, the more busily and persistently will they seek for flower-food, and the blossoms which after several days' waiting have at last opened to the warm rays of the sun, are now for the most part fertilized.' These words are not merely true for alpine flowers and insects, but are of universal application.

Beetles, most *Bees* and *Lepidoptera*, and also *Hover-flies*, permit of close approach during their visits to flowers, so that their movements can be accurately seen, and even the act of pollen transfer be observed. Other flies, especially *Muscidae*, are often so timid that they fly away at once when any one approaches the flowers in which they are busy, or they avoid settling on a flower when any one is near. In such cases it is necessary to watch the movements of these timorous guests through a telescope, preferably from a somewhat elevated position, or while lying on the grass.

Observations should be made as far as possible in the natural habitat of plants, as here the flower mechanisms and flower guests are in the original state, while a garden plant may have undergone slight modifications in its flower mechanism, while its visitors can only be recruited from insects which live in the garden or its vicinity. A pot plant or cut flower in a room, can of course only occasionally be visited by insects which fly through the open window, and its flower mechanism may then deviate very considerably from what is natural (cf. my note on *Parnassia palustris* in vol. II). On this point Sprengel ('Entd. Geh.') speaks as follows:—'We shall certainly not discover Nature's plan in the structure of flowers by taking the plant out of the garden or country. We must rather study flowers in their natural habitats—in short, *we must try to surprise Nature in the act.*'

After some experience it is possible without apparatus to catch many insects during their visits to flowers, for these guests are usually so busily employed in consuming the nourishment offered them, that they can be taken from the flowers by means of the fingers. Even the Syrphidae, which even with the help of a net are very difficult to catch when on the wing, may easily be taken on flowers¹. Other insects such as the Muscidae—as already mentioned—are very shy, so that they are secured with difficulty.

An observer should never omit to *draw*—in their various stages of development—the flowers of the inflorescences with which he has occasion to deal. Should his first few attempts fall short of complete success, practice will soon give him a sufficient amount of skill. It has always been very interesting to me to compare the first almost clumsy drawings of Hermann Müller with the later ones executed by him, which must be regarded as works of art. We may compare, for example, the almost diagrammatic outlines in his first work ('Fertilisation'), on p. 101 (*Nasturtium sylvestre* R. Br.), p. 107 (*Teesdalia nudicaulis* R. Br.), p. 132 (*Cerastium arvense* L.), p. 256

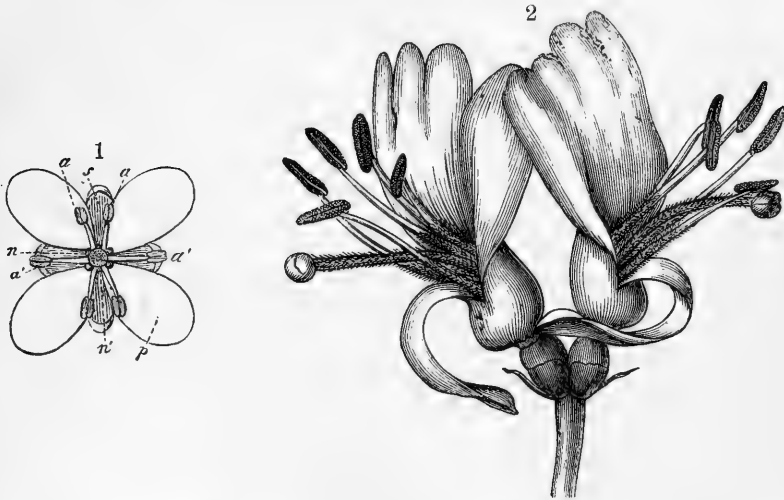


FIG. 78. (1) *Nasturtium sylvestre*, R. Br. (from Hermann Müller, 'Fertilisation,' p. 101). (2) *Lonicera nigra*, L. (from Hermann Müller, 'Alpenblumen,' p. 394).

(*Lythrum Salicaria* L.), p. 426 (*Lycium barbarum* L.), p. 386 (*Hottonia palustris* L.), p. 300 (*Galium Mollugo* L.), and so on, with the finely executed and beautiful illustrations in his second great work ('Alpenblumen'), e.g. on p. 394 (*Lonicera nigra* L.), p. 395 (*Lonicera alpigena* L.), p. 406 (*Phyteuma*), p. 470 (*Valeriana montana* L.), and so forth (see Fig. 78).

I have tried to photograph inflorescences, and this kind of reproduction has the advantage over a drawing that it gives a convincing picture which is true to nature. But an observer cannot always have photographic apparatus with him, nor can he everywhere perform the necessary operations. Besides which there are so many

¹ Knuth, 'Über blütenbiologische Beobachtungen,' Heimat, Kiel, iii, 1893, Part 5-6, pp. 8-9.

difficulties in photographing most very small objects that I now employ this method only under exceptional circumstances (cf. the illustration of the positions of flowers of *Lycium barbarum* L. in Fig. 79).

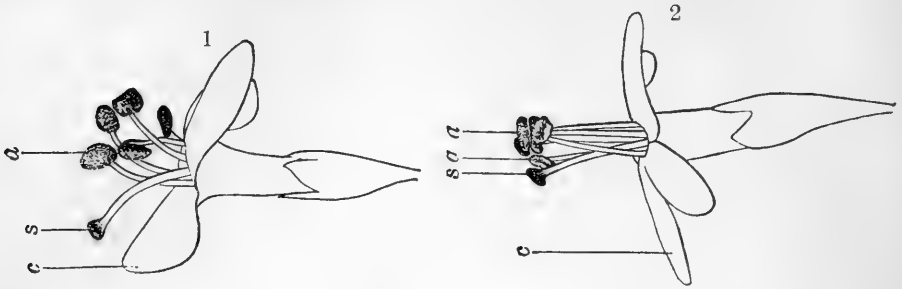


FIG. 79. *Lycium barbarum*, L. (from a photograph three times the natural size). (1) Flower in the first condition: the filaments of the dehiscent stamens are upwardly directed, the style with the stigma ready for pollination is bent down. (Condition for cross-pollination.) (2) Flower in the second condition: stamens and stigma are so close together that spontaneous self-pollination results from direct contact. c, corolla; a, anther; s, stigma.

I have therefore returned to the habit of drawing flowers. A drawing gives a better idea of what is seen than the best description.

Like all research, the study of the 'most interesting branch of lovable science'—Flower Pollination—is full of trouble. But the labour bestowed is amply repaid by the result, by deep penetration into the 'secrets of the flowers.' 'Each one of the beautiful flower faces,' says Hermann Müller ('Alpenblumen,' p. 23), 'which we were wont to marvel at with a sad feeling of resignation as so many mysteries for ever veiled, now looks upon us inspiring hope, and stimulating us in friendly wise to cheerful perseverance, as if it would say,—Only venture to come to me, and in true love make yourself acquainted with me and all my conditions of life, as intimately as you may, and I am ready to let fall the veil that hides me, and to trust myself and all my secrets to you!'

SUPPLEMENT TO THE INTRODUCTION.

1. Joseph Gottlieb Kölreuter.

I AM here able to supplement and correct the brief account of Kölreuter that I quoted at the beginning of the Introduction (p. 1) from Sachs's 'History of Botany' (Eng. Ed., p. 406, note), for Dr. J. Behrens of Karlsruhe has kindly placed at my disposal his own copy of his work 'Joseph Gottlieb Kölreuter, ein Karlsruher Botaniker' (Karlsruhe, 1894). Kölreuter was born on April 27, 1733, and was the eldest son of Johann Konrad Kölreuter, an apothecary at Sulz on the Neckar. Though nothing is known with regard to his early years it may be assumed that—encouraged by his father—he acquired a knowledge of the flora and fauna of his own neighbourhood when he was still a boy. In 1748 he went to the University of Tübingen, and in 1753 to Strassburg, returning in 1754 to Tübingen, where in the following year he took the degree of Doctor of Medicine, the title of his thesis being—'Dissertatio inauguralis medica de insectis coleopteris necnon de plantis quibusdam rarioribus (cum icones).'

Soon after he graduated (1756) Kölreuter went as an assistant in Natural History to the Imperial Academy of Sciences at St. Petersburg, where he made his first (fruitless) experiments on hybridization (1759), employing *Hibiscus trionum* and *Pentapetes phoenicea*, *Hibiscus trionum* and *Gossypium herbaceum*, *Atropa physaloides* and *Physalis Alkekengi*. While he was in St. Petersburg his 'Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen und Beobachtungen' (i.e. Preliminary Communication on some Researches and Experiments regarding the Sex of Plants) appeared, and he also published a number of zoological memoirs.

In the summer of 1761 Kölreuter returned to his home. In the course of the return journey he visited Berlin in the month of August, and there became acquainted with Johann Gottlieb Gleditsch, who had succeeded some ten years before in effecting the artificial fertilization of *Chamaerops humilis*. From Berlin Kölreuter went for a few weeks to Leipzig, and coming into contact with the botanists there, especially Christian Gottlieb Ludwig, received a new stimulus to research, and after his return to Sulz continued his experiments. In 1762 Kölreuter settled at Calw in Würtemberg, where he still carried on investigations on the sexual relations of plants. While the preface to his 'Vorläufige Nachricht' was written in Leipzig, and published by Gleditsch in Leipzig at the instigation of his friends there, the 'Fortsetzung' (i.e. Supplement), and also the 'Zweite Fortsetzung' (i.e. Second Supplement) are essentially the fruit of his labours in Sulz and Calw.

In 1763 Kölreuter was called to Karlsruhe by the margrave Karl Friedrich of Baden-Durlach, as overseer and director of the Royal Gardens, and Professor of Natural History. In the beginning of 1764 he assumed these offices, and the 'Dritte Fortsetzung der vorläufigen Nachricht' (i.e. Third Supplement to the Preliminary Communication) appeared as the result of his first two years' work in Karlsruhe.

Owing to the disaffection of the gardeners placed under him, it became impossible for Kölreuter to retain his offices. He continued his experiments on hybridization in his private garden up to 1776. He then took a house which had no garden connected with it, so that he ceased to have opportunity for making such experiments. He died on November 11, 1806. A list of his other botanical works is given in the Bibliography of Flower Pollination.

2. How Flowers attract Insects.

While volume I of this handbook of Flower Pollination was in the press there appeared five parts of a treatise by Félix Plateau entitled '*Comment les fleurs attirent les insectes. Recherches expérimentales*' (i.e. How Plants attract Insects. Experimental Investigations)¹. These may well attract our serious attention, for the conclusions which Plateau draws from his experiments are such as to shake belief in a view that has hitherto prevailed as a fundamental oecological law. As already stated in a preliminary communication made to the '*Naturwissenschaftlicher Verein für Schleswig-Holstein*' (Schleswig-Holstein Society of Natural Science) on Feb. 14, 1898, and in a paper in the '*Botanisches Centralblatt*' (lxxiv, 1898, pp. 39-46), I do not agree with Plateau's conclusions, but interpret his experiments in an essentially different way.

The first communication by Plateau on this subject is known to me only from reviews. The author wrote me that he had no spare copy to give because too few reprints of the paper had been struck off, and his supply of them was exhausted. According to the review by Kienitz-Gerloff in the '*Botanische Zeitung*' of April 16, 1896 (lxvi, pp. 123 and 124), Plateau limited himself almost entirely in the first part of his treatise to the results of investigations he had carried out on dahlia flowers which were not in full bloom. He covered in some instances only the ray-florets, in others both ray- and disk-florets, partially or completely with papers of various colours, or with leaves of the same green as those of the dahlias. From the number of insect visits made to the flowers—by species of *Bombus*, *Megachile*, *Pieris*, and *Vanessa*—during the space of an hour, Plateau arrived at the following preliminary conclusions with regard to ligulate Compositae—conclusions which are repeated in the second part of his memoir:—

1. Insects actively visit unmutilated inflorescences when the form and colour of the florets are masked by green leaves.
2. The form and bright colours of the capitula do not appear to exercise an attractive influence.
3. The coloured ray-florets of single dahlias—and consequently of other ligulate Compositae—do not play the part of a flag or signal as has hitherto been supposed.
4. The forms and colours of flowers do not appear to serve as means of attraction, but insects are apparently guided to the capitula of Compositae by some sense other than sight, probably by smell.

¹ Bull. Acad. roy., Bruxelles, Series 3, xxx, 1895, pp. 466-88; xxxii, 1896, pp. 505-34; xxxiii, 1897, pp. 17-41; xxxiv, 1897, pp. 601-44 and pp. 847-81.

Kienitz-Gerloff rightly makes the following remarks on this (Bot. Ztg., lxvi, 1896, pp. 123 and 124).—‘Both premisses and conclusions are equally open to attack. For of course the covered dahlia heads could still attract animals by their odour—though this might not be perceptible to human beings—and to infer from this that the colour of uncovered flowers plays no part in attracting insects is the less justifiable as Plateau gives absolutely no comparative figures with regard to such visits, but only makes the very indefinite statement that insects flew to the covered flowers in the same way as to the uncovered, without hesitation and with equal eagerness.’

In the introductory words to the second part of his memoir, Plateau gives prominence to the fact that—his results being so diametrically opposed to existing views—he had continued his experiments on the question how flowers attract insects partly in his own garden, partly in the country, and partly in the Botanic Gardens at Ghent, where he had both repeated the experiments of other investigators and made entirely new ones.

Of all Plateau’s researches those communicated in this second part appear to me to be the most important. In these he made use of flowers which had been rendered very inconspicuous by *removal of the petals, or of the coloured part of the corolla*, but which nevertheless received a very considerable number of insect visits. But before considering these researches in detail I should like first to deal with the other and less important experiments of this investigator.

Plateau first repeated the experiments on dahlias with *Heracleum Fischerii* (Umbelliferae), by covering its umbels with rhubarb leaves. Yet within thirty minutes he observed three visits from *Apis mellifica* var. *ligustica*, two from other small bees, one from *Calliphora vomitoria*, and one from *Phyllopertha horticola*, followed in a further period of an hour and a half by twenty-five from *Odynerus quadratus*, ten from *Prosopis communis*, three from *Calliphora vomitoria*, and one from *Musca domestica*.

In my opinion this only proves that the insects named are *also* attracted by odour, which has been disputed by none of the recent oecologists. No proof has been afforded that the attraction is *only* by odour, for no control experiments were made with uncovered umbels. From the fact that many insects (*Apis*, *Andrena* sp., *Bombus* sp., *Megachile ericetorum*, *Pieris napi*, *Vanessa C. album*, *Eristalis*, and the smaller *Syrphidae*) showed themselves *indifferent as regards the various colours* of varieties of the same species, or of the species of the same genus, visiting without displaying preference the blue, white, purple, and rose-red flowers of *Centaurea Cyanus*, the red, purple, rose-red, orange, and white capitula of *Dahlia variabilis*, the purple, rose-red, and white capitula of *Scabiosa atropurpurea*, the red flowers of *Linum grandiflorum* and the blue ones of *L. usitatissimum*, Plateau concludes that the colours of flowers cannot play any part in the attraction of insects. He also cites the similar observations of other investigators, e.g. Darwin saw a humble-bee pass from a red *Dictamnus Fraxinella* to a white-flowered one, and another betake itself from one variety of *Delphinium Consolida* to another that was differently coloured, while much the same thing was noticed by Gaston Bonnier for the colour varieties of *Althaea rosea*, *Digitalis purpurea*, and *Brassica oleracea*, as well as by Errera and Gevaert for species of *Pentstemon*.

In none of these cases is Plateau justified in the general inference that the colours of flowers play no part in attracting insects. The only conclusion to be drawn is that in *flowers of the same shape* the colour is a matter of indifference to the visitors, and that these possess an exceedingly well-developed sense of form. The honey-bee, as is well known, and as Hermann Müller repeatedly points out, after once making a beginning keeps with great constancy to one species of flower, sucking this alone to the exclusion of all others which may be present. And that in this it is *not guided by odour but by colour and form* appears from the circumstance that it often makes indiscriminate visits in the case of flowers that are similarly formed though of different species, e.g. *Sinapis arvensis* and *Raphanus Raphanistrum*, which cannot, however, be supposed to possess the same odour.

The fact that according to Plateau's further experiments very conspicuous flowers, which as a rule receive few visitors (e.g. *Pelargonium zonale Willd.*, *Phlox paniculata L.*, *Anemone japonica Sieb. et Lucc.*, *Convolvulus sepium L.*), attract large numbers *when honey is put upon them*, only proves that the odour of honey exercises a great power of attraction upon insects, which has long been known. It is only necessary to place honey anywhere to secure the immediate appearance of numerous insects which are fond of it.

In a similar way may be explained Plateau's numerous experiments on anemophilous flowers, by adding diluted honey to which numerous insects were attracted. When Plateau further proved that insect visits ceased after *removal* of the nectar-producing structures (of dahlias), but began again when nectar was reintroduced—*Bombus*, *Megachile*, and *Vespa* making their appearance—he confirmed the well-known fact that insects can accurately distinguish between the nectarless and nectar-yielding flowers of a given species. On this point Hermann Müller writes as follows ('Weitere Beobachtungen,' III, p. 13):—'Honey-bees and humble-bees when despoiling *Cerinthe* minor display their great skill in recognizing small differences between flowers. Some of the flowers that have been visited, and in which the pyramid of stamens is pressed apart at the apex, they fly past without touching, others they touch in passing only to leave again immediately. They fly with extended proboscis, humming as they go, and steadily searching from flower to flower, till they have found one filled with nectar.' From this it appears that insects can see extremely well at a short distance, and that they are led by sight to the flowers they visit.

The recognition of artificial flowers by insects obviously depends upon this *appreciation of very minute differences*, and involves *both sight and smell*. It is accordingly not to be wondered at that insects should not have visited the artificial flowers of *Ribes sanguineum Persh.*, *Persica vulgaris Mill.*, *Cerasus vulgaris Mill.*, *Myosotis alpestris Schm.*, *Pyrus Malus L.*, *Saxifraga umbrosa L.*, *Digitalis purpurea L.*, and *Lathyrus latifolius L.*, which were placed by Plateau among natural flowers of the same species, but left them unheeded, even when provided with honey. Though these artificial flowers may seem very realistic to human eyes, yet insects are not to be deceived, for the surface of such flowers appears quite different on close inspection from that of natural ones, and their odour—due to the materials of which they are made—is easily perceived by insects, though perhaps not by us.

Two causes, one due to sight, the other to smell, prevent insects from visiting artificial flowers, just as—according to the observations of Hermann Müller on

Cerinth minor—they are kept away from natural flowers that have already been visited. Plateau on several occasions observed 'inspection flights' of certain insects, which were to be regarded as undertaken for the purpose of making observations, and not as 'smellings' at the artificial flowers in order to test them. For example, a bee on *Saxifraga umbrosa* undertook 'un vol ascendant d'inspection devant une des grappes imitées,' and again, 'Une seule *Melanostoma mellina* a volé un instant devant la grappe miellée.' Plateau remarks with regard to *Lathyrus latifolius* that bees of the species *Megachile ericetorum* paused a moment in their flight on encountering the artificial flowers, but never settled upon them—'Les insectes ont tournoyé un moment, dans un but d'examen, autour des grappes artificielles, sans, du reste, jamais tenter d'entrer dans une de ces fleurs.'

Only the Muscidae—long ago described as 'stupid' by Ch. K. Sprengel—now and then allow themselves to be deceived, or go after honey which has been hidden in artificial flowers. Artificial apple-blossoms, for instance, were visited by *Calliphora* and *Musca*, and a specimen of *Calliphora* crept into an imitation flower of *Digitalis purpurea* into which honey had been put.

Plateau himself thought that there might possibly be slight differences between the colours of artificial and natural flowers, deterring insects from visiting the former. He therefore made artificial flowers by folding up green foliage leaves and fixing in them a small sponge saturated with honey. *Apis*, *Musca domestica*, *Calliphora vomitoria*, *Sarcophaga carnaria*, *Lucilia caesar*, *Odynerus quadratus*, and *Bombus terrester* at once made their appearance for the purpose of enjoying the honey. As already pointed out, there is nothing remarkable about this, for it is well known that insects are strongly attracted by the odour of honey.

But for other odours the results are quite different. When Plateau added to honey a drop of essence of lavender, thyme, sage, mint, orange, or bergamot, there were no insect visits. Even when he employed very dilute solutions of these odorous substances but few insects were attracted. The following inferences can be drawn from these facts:—

1. The essences employed have a relatively small attractive power.
2. A few of them (mint) are even repellent.
3. Only the essences of thyme and sage are feebly attractive.

From these experiments it follows that solutions of odoriferous plant extracts, which according to Plateau ought to attract insects, do not do so. His theory is therefore refuted by his own experiments.

Plateau further adduces the case of numerous *green, greenish, brown, or brownish flowers or inflorescences* which are visited and pollinated by insects, but this merely proves that insects are guided to inconspicuous flowers by odour, not that colour is of no importance. Plateau has not compared the frequency of insect visits to inconspicuous and conspicuous flowers of the same size, and it is only experiments of this kind which can help to settle the point at issue.

As already mentioned, those experiments of Plateau in which he prepared *inconspicuous mutilated flowers by removing the petals or the coloured part of the corolla*—with the result that even then they received a great many insect visits—demand full consideration. As mentioned in my 'Vorläufige Mitteilung' (i.e. Preliminary Communi-

cation), I was at first more than surprised to hear of these experiments, for they seemed entirely to overthrow a view which I had up to that time considered an established oecological fact. But on careful consideration of these experiments, I came to the conclusion that Plateau's inferences are not justified, and that another explanation is permissible. Let us take the experiment made with *Digitalis purpurea*. Plateau cut away not only the corolla-tube but also the style and stamens, till only a stump 1 cm. long remained (see Fig. 80). Gaston Bonnier ('Les Nectaires,' 1879, p. 61) observed many years ago that 'les abeilles continuent à visiter en même nombre les Digitales sur les pieds où toutes les couronnes avaient été enlevées.' Plateau's experiments confirmed this observation, for the visitors of uninjured flowers (*Bombus terrester* L. and *Anthidium manicatum* L.) also sucked the mutilated ones, finding it hard work to hold on while doing so—the resting-place presented by the complete corolla being absent. 'Ainsi,' says Plateau, 'les hyménoptères visitent encore, et

d'une façon effective, les fleurs de Digitales n'ayant plus ni leur couleur attractive, ni des dimensions les rendant très visibles, ni la forme que ces animaux ont coutume d'utiliser pour parvenir aisément au nectar.'

But if we remember that a mutilated flower is an open cup, containing nectar which is constantly renewed from the base of the flower—where the nectar is situated—we shall realize that this nectar is freely displayed after removal of the corolla, and therefore—being exposed to the direct action of sunshine and wind—must evaporate more quickly, give out a stronger odour, and attract more strongly than when it is hidden at the bottom of a long corolla-tube. The visits of insects to this exposed nectar-cup would therefore be more numerous than those to the uninjured flower, assuming that the corolla-tube has no significance as a means of

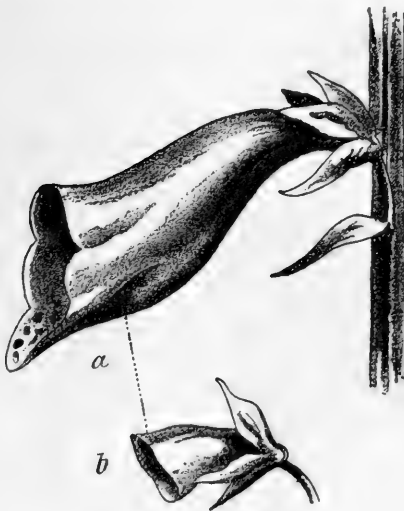


FIG. 80. *Digitalis purpurea*, L. (after Plateau). a, complete flower; b, mutilated flower.

attraction. No such observation, however, is found in Plateau's account, so that the uselessness of the brightly coloured corolla for the purpose of attraction is not proven.

Plateau has also made similar experiments to those on *Digitalis* with *Lobelia Erinus*, *Oenothera biennis*, *Ipomoea purpurea*, *Delphinium Ajacis*, and *Antirrhinum majus*. As before he removed the conspicuous part as far as possible, and yet the inconspicuous remnants—except in the case of *Antirrhinum majus*—received visits from insects sometimes almost as frequently as the complete flowers. Plateau explains that this is due to the fact that odour alone is the means of attraction. In my opinion the mutilated flowers should here again have received more numerous visits than the uninjured flowers, as in the former the odour of nectar must have been stronger. Since the mutilated flowers were not visited so frequently as those

that were uninjured, it follows that the brightly coloured corolla exerts an attractive influence.

It was only in the case of *Antirrhinum majus* that the mutilated flowers received no visitors. After Plateau had cut down a number of such flowers till they were only 1 cm. long, the humble-bees (*Bombus terrester* L.) which were sucking the uninjured blossoms showed no inclination to visit them. Plateau tries to explain this by saying that in order to reach the nectar of the mutilated flowers—which are open above—by flying up from below, the insects could get no foothold except by suddenly converting their ascending movements into descending ones. For this reason they preferred to forgo the use of the nectar in the mutilated flowers, and to seek out uninjured blossoms in the neighbourhood.

This explanation does not seem to me to be a happy one, because these insects settle on many other flowers from above, without suffering any inconvenience from this mode of alighting. It appears to me far more probable that *the odour of Antirrhinum majus is not sufficient for purposes of attraction*, but that here *the form and colour of the corolla play a leading part* in this matter, so that the insects do not visit mutilated flowers in which these means of allurement are wanting.

Plateau conducted a most interesting experiment with *Centaurea Cyanus*. He removed the blue ray-florets—which according to our view merely serve to attract and are therefore neuter—leaving only the rather inconspicuous disk-florets (see Fig. 81). In spite of this many bees (*Megachile ericetorum*) visited the cornflowers so treated. Plateau supposes that the insects were attracted by the odour. I believe that this occurrence is quite as easily explained by assuming that the visitors of intact cornflower capitula have become acquainted with the form of the nectar-yielding disk-florets, and are able—from a short distance—to recognize them after the removal of the ray-florets just as well as before.

Friedrich Dahl, among others, has proved that insects are able to distinguish forms accurately at a short distance (cf. Zool. Anz., Leipzig, xxii, 1889). Professor Dahl told me of the following observation, which can only be explained on the assumption that insects are guided by the sense of sight.—The young honey-bees that appear in spring settle upon flowers with nectar beyond their reach owing to the depth at which it lies, and make vain attempts to suck it. Older bees (that have already swarmed), on the other hand, come near such flowers, but turn away without settling on them. This must be due to the fact that the older bees having learnt that the nectar of these flowers is not within their reach, look at them on getting near and realize that there is nothing to be had. Were it the specific odour of the flowers that deterred them from visiting they would not need to go so

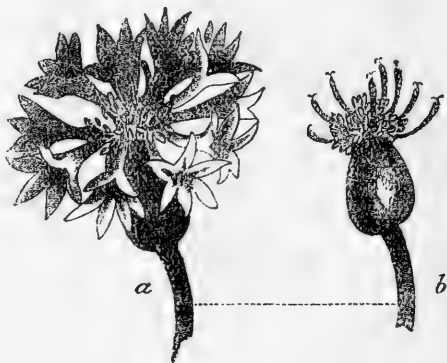


FIG. 81. *Centaurea Cyanus*, L. (after Plateau). *a*, Capitulum with ray-florets; *b*, capitulum without ray-florets.

near, but would be able to perceive it at a greater distance, and would then turn aside.

The observation of Delpino, mentioned on p. 141 of this volume, can likewise only be explained by reference to the visual power of insects, and I therefore repeat his description.—On a meadow in Vallombrosa there were numerous plants of *Bellis perennis* and *Anemone nemorosa*, equally mixed, and distributed at about equal distances from one another. Delpino saw a bee collecting pollen zealously from *Anemone*. When flying from one flower to another it repeatedly made a mistake and went to flowers of *Bellis*, though on reaching these recognized its error, and at once flew on again.

Plateau has given a very one-sided interpretation to his experiments, without regard to the earlier observations of other investigators. For instance, he quite overlooks the experiments of Forel, who proved that blinded insects could not recognize the part of a flower on which they wished to settle, while others from which he had removed the antennae—which bear the olfactory organs—flew with certainty from flower to flower.

Plateau further entirely ignores the results of the observations of Hermann Müller, which have been fully confirmed by the statistical investigations of E. Loew, J. MacLeod, and myself. By these the following conclusions have been established:—

1. Other things being equal, a flower is visited by insects in proportion to its conspicuousness. Among nearly allied species which agree closely in the form and colour of their flowers, and naturally also agree in their floral mechanisms, those which are most conspicuous receive the most numerous visits, while those which are least conspicuous have the smallest number of visitors¹.

2. In a number of cases odour has more to do with the attraction of insects than the size and colour of the corolla. 'The richly scented flowers of *Convolvulus arvensis*,' says Hermann Müller ('Fertilisation,' p. 572), 'are far more abundantly visited than the larger and more conspicuous but scentless flowers of *C. sepium*; the sweet-scented violet is much more visited than the larger, brightly coloured, but scentless pansy; the small, insignificant, but strongly perfumed flowers of *Lepidium sativum* surpass in the abundance of their visitors the other more conspicuous but scentless Crucifers.'

3. Dull yellow flowers (*Bupleurum*, *Anethum*, *Pastinaca*, *Alchemilla*, and others) are not visited as a rule by beetles, while nearly related flowers that are white, or of some other conspicuous colour, attract these insects even when nectarless (e.g. *Helianthemum*, *Papaver*, *Genista*). Reddish blue or violet flowers are preferred by bees, butterflies, and hover-flies, which are highly specialized visitors, while the insects that appear most frequently on white or yellow flowers have a short proboscis, and are unskilled visitors. Bees with a long proboscis (humble-bees) appear to be least dependent upon the colour of flowers. As Hermann Müller expresses himself ('Alpenblumen,' p. 496), 'these—the most intelligent of flower

¹ H. Müller ('Fertilisation,' p. 570) gives as examples species of *Ranunculus*, *Geranium*, *Malva*, *Polygonum*, *Stellaria*, *Cerastium*, *Epilobium*, *Rosa*, *Rubus*, *Veronica*, *Carduus*, *Hieracium*, and the various flower-forms of *Euphrasia officinalis*, *Rhinanthus Crista-galli*, and *Lysimachia vulgaris*.

guests—are influenced in the choice of flowers, even more by food-value than by external appearance.’

4. The strong-smelling flowers of Ruta, Anethum, and the like, attract flies more particularly. The species of Prosopis, which themselves have a peculiar odour, display marked preference for strong-smelling flowers (Reseda, Lepidium, Ruta, Anethum, Achillea, Matricaria). Sweet aromatic odours (Thymus, Lavandula, Rosa, and others) strongly attract bees without excluding other insects. The odour—not strongly exhaled till towards evening—of many white flowers with long corollatubes (Loniceria Periclymenum and Caprifolium, Melandryum album, and the like), attracts hawk-moths (Sphingidae) and other crepuscular and nocturnal Lepidoptera. Flowers with the odour of carrion specially attract carrion-flies, and the urinous odour of Arum attracts moth-flies (Psychodidae).

Numerous facts in Flower Pollination support the view that the corolla plays a prominent part in attracting insects. First let us ask ourselves why else does it exist, why are flowers provided with bright and varied colours if not for the purpose of alluring insects? Why, let us ask further, are the male flowers of diclinous plants larger than the female flowers if not to attract by their greater conspicuousness the earlier visits of insects, so that the female flowers may be pollinated? What can be the object of the remarkable change of colour in flowers that have been fertilized (e.g. Ribes sanguineum, R. aureum, Weigelia rosea, Melampyrum pratense, Aesculus Hippocastanum, and so forth) unless to render more conspicuous the entire inflorescence? And many more such questions might be propounded.

Plateau's experiments only show that the sense of smell perhaps guides insects to a greater extent than has hitherto been supposed. Apparently there is need of further experiment to decide questions as to the attraction of insects to flowers by means of the senses of smell and sight. Meanwhile the following law may be provisionally accepted.—*Attraction from considerable distances is certainly effected for the most part by the odour of the flowers, which fills the air as with invisible clouds, and indicates the direction for flight: when the insects approach nearer (1–2 m.), the colours of flowers undertake the task of attracting them further, and when they finally settle, the lines and points long since described by Sprengel under the name of ‘Saftmal’ (i.e. sap-mark) serve to point out the way to the nectar.*

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OF

FLOWER POLLINATION

[The abbreviations employed by the author have been replaced, where possible, by the standardized ones given in the 'International Catalogue of Scientific Literature—List of Journals and Supplementary List of Journals, London, 1903 and 1904.' A slight departure, however, has been made by putting the place of publication at the *end* in all cases. Small Roman numerals (e. g. xxiv) are used to indicate *Volumes*, except in the case of books or memoirs separately published, for which large Roman numerals (e. g. II) are employed. When two dates are given, the first—in ()—is the title year, and the second the actual year of publication,—e. g., *Justs bot. Jahresber.*, Leipzig, i, (1873) 1874. Certain periodicals—e. g. *Series 1* of 'The Gardeners' Chronicle and Agricultural Gazette,' London—have no volume numbers, and are therefore only indicated by the *year* of publication. The abbreviation *Ab.* is used for 'Abstract,' 'Abstracts,' 'Review,' or 'Notice.'—Tr.]

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49. An entomological tour on the table-land of Mount Arthur. (An interesting account of the alpine Lepidoptera, especially the micro-Lepidoptera. The colouration became markedly darker with increasing altitude. Flies (*Calliphora quadrimaculata*, *Sarcophaga laemica*, and others) were very numerous on the summit. *Vanessa gonerilla* and *Chrysophanus* are still present at 3200 feet above the sea-level: the greatest altitude is attained by *Erebia pluto*.) *Op. cit.*, xxii, 1890, pp. 179-86.
50. On entomological field-work in New Zealand. (The best months for collecting forest-insects are November, December, and January. Many of the forest Lepidoptera are coloured green, and thus harmonize with the mosses that thickly carpet the ground. Among other localities, Arthur's Table Mountain in the Nelson district, Mount Cook, and the Humboldt ranges, possess a rich mountain flora and fauna. The insects of the last-named include the rare *Erebia butleri* and the extraordinary Ichneumonid *Rhyssa antipodum*. Of flower visitors a Geometrid (*Gonophylla nelsonaria* *Feld.*) on *Metrosideros*, and Noctuidae on *Veronica*, are mentioned.) *Op. cit.*, xxxiii, 1900, pp. 383-405.
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56. Our migratory Birds. (*Zosterops coerulescens* *Blyth* (= *Z. lateralis* *Lath.*) has

- migrated into New Zealand since 1856, and has reached as far as the Auckland, Chatham, and Campbell Islands. It must therefore have crossed Bass Strait, which would involve continuous flight for 24-36 hours.) *Op. cit.*, xxxiii, 1900, pp. 251-64.
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59. Additions to the Diptera Fauna of New Zealand. (The numbers of sp. are as follows.—Psychodidae, 3. Chironomidae, 12. Tipulidae, 6. Rhyphidae, 1. Mycetophilidae, 2. Bibionidae, 5. Asilidae, 1. Agromyzidae, 1.) *Op. cit.*, xxxiv, 1901, pp. 179-96.
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are white, 10 green, 13 yellow, 6 dark yellow, 7 purple and red, 1 blue: the inconspicuous flowers of Restiaceae, Cyperaceae, and Gramineae not being taken into consideration. There is a greater poverty of flower-visiting insects in the Alps of Australia than in those of Europe.) *Vict. Nat.*, Melbourne, xx, 1903, pp. 64-70.

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